SEED SOURCE VARIATION: ASSESSMENT OF POTENTIAL FOR IMPROVING PLANTATION FORESTRY IN RWANDA

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DECLARATION

I, the undersigned, hereby declare that the work contained in this thesis is my own original and has not previously, in its entirety or in part, been submitted at any university for a degree.

Signature. Date

ABSTRACT

Nine species in ten different seed source trials were evaluated with the aim of understanding their potential as exotics in improving plantation forestry in Rwanda. Assessment was based on tree growth and stem quality, juvenile-mature and trait-trait phenotypic correlations as well as the relationship of seed source performance and the locational variables of seed origin. *Eucalyptus saligna, E. urophylla, Pinus maximinoi* and *P. tecunumanii* proved to be very promising as plantation species and are highly recommended. *P. patula* and *Grevillea robusta* are also recommended for plantation and agroforestry purposes respectively. *P. caribaea* and *P. kesiya* proved to be very poorly adapted under local conditions and should be retested if resources were available. All trials except *E. urophylla,* and *P. maximinoi* (the two had very few degrees of freedom) showed significant differences of varying degrees in different traits between seed sources indicating their potential for genetic improvement through selection and breeding. Similarly, all trials except *E. urophylla,* and *P. maximinoi* indicated significant juvenile-mature phenotypic correlations of varying degrees in different traits, with height showing strongest relationships. On average, trait-trait relationship was observed to be strongest between diameter and volume, followed by height and volume, height and branching pattern, stem form and branching pattern, stem form and height, branching pattern and volume, and diameter (and volume) and stem form in that order. Based on juvenile-mature phenotypic correlations, tree height at 15 and 16 years can be predicted as early as at three years for *E. tereticornis* $(r \leq 0.4680)$ and *P. kesiya* $(r \leq 0.5530)$ respectively, while that at 14 and 16 years in *P. tecunumanii* $(r \leq 0.4820)$ and *P. patula* $(r \leq 0.5562)$ can be predicted using height at four years. This however may only be true where genetic and phenotypic relations are strong (as may be the case in *E. tereticornis* since high heritability estimates were obtained).

The following additional recommendations are made under this study: To study the effect of growth rate on wood properties of very fast growing pine species; to introduce other tropical species such as *E. deglupta* and *P. oocarpa* so as to diversify species; carry out studies to better understand the effect of altitude on the adaptability of the exotic tree species in the tropical and sub tropical environments and lastly, carry out genetic tests in future so as to ascertain the obtained results on age-age and trait-trait correlations in this study.

OPSOMMING

Nege spesies in tien verskillende saadbronproewe is geëvalueer met die doel om hulle potensiaal as eksotiese spesies te verstaan sodat plantasie-bosbou in Rwanda verbeter kan word. Die evaluering is gebaseer op boomgroei en stamkwaliteit, jongeling-volwasse en eienskap-eienskap fenotipiese korrelasies, sowel as die verhouding tussen saadbronprestasie en die omgewingveranderlikes van saadoorsprong. *Eucalyptus saligna, E. urophylla, Pinus maximinoi* en *P. tecunumanii* blyk baie belowend te wees as plantasiespesies en word sterk aanbeveel. *P. patula* en *Grevillea robusta* word ook aanbeveel vir die doeleindes van plantasie- en agrobosbou onderskeidelik. *P. caribaea* en *P. kesiya* blyk baie swak aangepas te wees onder plaaslike omstandighede en moes weer getoets te word, sou die hulpmiddele beskikbaar wees. Alle proewe (behalwe *E. urophylla* en *P. maximinoi* – dié twee het baie min vryheidsgrade gehad) het beduidende verskille van afwisselende grade getoon tussen saadbronne in verskillende eienskappe. Dit dui aan dat hulle potensiaal het vir genetiese verbetering deur seleksie en teling.

Eweneens het alle proewe behalwe *E. urophylla* en *P. maximinoi* beduidende jongeling-volwasse fenotipiese korrelasies van afwisselende grade in verskillende eienskappe getoon, met hoogte wat die sterkste verhoudings getoon het. Oor die algemeen was die eienskap-eienskap verhouding die sterkste tussen deursnee en volume, gevolg deur hoogte en volume, hoogte en vertakkingspatroon, stamvorm en vertakkingspatroon, stamvorm en hoogte, vertakkingspatroon en volume, en deursnee (en volume) en stamvorm, in daardie volgorde. Op grond van jongeling-volwasse fenotipiese korrelasies kan boomhoogte op 15 en 16 jaar op so vroeg as drie jaar voorspel word vir *E. tereticornis* (*r* 0 0.4680) en *P. kesiya* (*r* 0 0.5530) onderskeidelik, terwyl boomhoogte vir *P. tecunumanii* (*r* 0 0.4820) en *P. patula* (*r* 0 0.5562) op 14 en 16 jaar voorspel kan word op vier jaar. Dit kan egter net juis wees waar genetiese en fenotipiese verhoudings sterk is (soos die geval kan wees met *E. teretiornis,* aangesien hoë erflikheidskattings verkry is).

Die volgende addisionele aanbevelings word in hierdie studie gemaak: om die effek te bestudeer van die groeitempo op die houteienskappe van denspesies wat baie vinnig groei, te bestudeer; om ander tropiese spesies soos *E. deglupta* en *P. oocarpa* ook te betrek ten einde die spesies te diversifiseer; om studies uit te voer ten einde die effek van hoogte op die aanpasbaarheid van die eksotiese boomspesies in die tropiese en subtropiese omgewing beter te verstaan; en laastens, om

in die toekoms genetiese toetse uit te voer ten einde die resultate wat in hierdie studie op ouderdom-ouderdom en eienskap-eienskap korrelasies verkry is, te bevestig.

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DEDICATION

To my dear wife Yvonne and children Patrick and Pauline.

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1. INTRODUCTION

Rwanda is a very small, landlocked country (26 338 km²) in the east central African region. It shares boundaries with Burundi (south), Democratic Republic of Congo (west), Tanzania (east) and Uganda (north). It is densely populated with 8 million inhabitants, a population density of about 300 inhabitants per km², with the population growth rate of about 3.1% (MINAGRI, 1998). As its population is growing very fast, the natural forest resources are diminishing at an alarming rate. Nyungwe forest reserve has decreased from 114 000 ha in 1958 to 90 000 ha in 2 000 (Gapusi, 2000) and Akagera national park from 250 000 ha in 1997 to 90 000 ha in the same year (Ndayambaje, 1997). Rate of decrease of natural forests and forest reserves in the country for about 40 years are given in Table 1.1. Consequences of the high deforestation rate are many, some of which include the extinction of some species and ecosystems, an increasing wood deficit, land degradation and environmental instability. A bibliographic review by Gapusi and Mugunga (1999) based on old literature reveals more than 150 plant species that are rare and threatened by extinction in the country.

National wood consumption rate of 6.2 million m^3 per year (0.91m^3 per inhabitant per year) was estimated in 1987 (Iyakaremye, 1987) and 2.85 million m^3 per year in 1990 (Munyarugerero, 1990). The big difference between the figures may partly be due to the increased rate of afforestation and partly due to imprecise estimation. Although no current information regarding wood consumption rate is available, it is expected to have increased significantly since the population has increased by half a million and wood utility is being diversified with time.

Wood makes the main source of energy in the country. MINAGRI (1998) estimates national sources of energy to be wood (97%), electricity (2%) and other (1%). Rural and urban populations consume wood as firewood and charcoal respectively. Kalinganire (1992) estimates national wood consumption distribution as firewood 91.3%, for industrial use 4.7%, for construction 3.5% and sawn timber 0.5%. Wood consumption by wood based industries is

expected to increase since both governmental and private entrepreneurs are likely to increasingly invest in the sector.

Table 1.1: Rate of decrease of natural forests, national parks and game reserves in Rwanda during the period 1960-1999.

Forest	Year						% Decrease
	1960	1970	1980	1990	1996	1999	
Nyungwe	114,025	108,800	97,000	97,000	94,500	89,150	21.8
Gishwati	28,000	28,000	23,000	8,800	3,800	-	100
Mukura	3,000	3,000	2,000	2,000	1,600	1,600	46.7
Birunga	34,000	16,000	15,000	14,000	12,760	12,760	62.5
Akagera	267,000	267,000	267,000	241,000	220,000	90,000	66.3
MPA*	64,000	45,000	45,000	34,000	22,000	-	100
ESW**	150,000	150,000	90,000	50,000	20,000	-	100
Total	660,025	617,800	539,000	446,800	374,660	193,510	70.1

***Mutara Protected Area **Eastern Savannah Woodlands in Kibungo and Bugesera areas**

Source: MINAGRI (1999)

As a result of limited supply of wood from natural forests, some wood and wood based products are imported from neighbouring countries like Congo and Tanzania (Kalinganire, 1992; Iyakaremye 1987). Plantation forestry makes an important complement of the natural forests for the supply of wood for various purposes. Plantations are established and managed to produce wood for specific products - sawn timber, wood fuel, fibres, etc. Productivity is expected to be higher in plantations than in natural forests since, apart from species selection and other breeding activities depending on purpose, growing conditions are also better in plantations.

Species grown in plantation forestry are mostly exotics due to the fact that they are extensively studied for various characteristics like adaptability, growing conditions, silviculture, management, wood properties in relation to utilization, etc. Wright (1976) gives several reasons for expecting success from plantations and these include both growing and non-growing factors.

Plantation forestry in the country started by introduction of exotics by Missionaries in 1900`s (Kalinganire and Hall, 1993) and more specifically in 1920 (Mihigo, 1999). Three hundred and eighty hectares of plantations were established by 1920, 12 000 ha between 1920 and 1960, 17 000 ha by 1965 and 23 500 ha by 1968 (Kalinganire, 1992). In 1980, the total plantation area was

estimated at 25 000 ha (Michelson, 1969; 1970; Birori, 1982 and Kalinganire, 1988). The area is estimated to be 247,500 ha and 256,300 ha in 1991 and 1997 respectively (FAO, 1999 and Mihigo, 1999). This matches with the projection that by the year 2000 total plantation area would be 250,000 ha (Iyakaremye 1987) following an annual planting of 10,000 ha as reported by Mutungirehe (1987).

As seen above, many authors report different areas under plantation in Rwanda as well as the national wood deficit. What matters is that plantations have been increasing and that wood deficit also increased with time.

Studies regarding species adaptability started at their introduction in Rwanda. A 200 ha arboretum was established in 1934 by the colonial administration in Butare Province. This was aimed at studying species adaptability and monitoring their performance so as to produce wood that would satisfy the needs of their territory (Rwanda - Urundi). Due to the fact that Eucalypts were known for their rapid growth by the time, 69 *Eucalyptus* species were introduced in the arboretum together with other species at its establishment. Reports on adaptability of *Eucalyptus* and *Pinus* spp. is given by Denis (1958) and Reinders (1962). Coster and van Bellingen (1976) and Gasana (1980) also report on the adaptability of some exotic tree species in Rwanda.

Interesting results as regards to adaptability, growth, silviculture and management of some exotic tree species were achieved from the arboretum. Seed collection from the arboretum has continually been done for afforestation both locally and for export to neighbouring countries such as Burundi and The Democratic Republic of Congo. Conclusions made from studies in the arboretum on exotics are however limited since it is situated in only one of seven seed zones in the country. Seed collection from the arboretum may be genetically poor since each species is grown in a small plot (0.25 ha). Related species of *Eucalyptus* are planted very close to each other with a consequent high risk of hybridisation. Therefore seed from such sources may hardly be of pure species. To obtain reliable results in relation to exotic species performance to different agro-ecological zones in the country, provenance experiments for main and promising exotic species were established and managed in 1980`s by the "Centrale des Graines Forestieres,

(CGF)" of The "Institute des Sciences Agronomiques du Rwanda, (ISAR)." Other breeding activities aimed at improving forest productivity such as selection, establishment and management of seed stands were also done for some exotic tree species.

Due to the small size of the country, only small areas are available for plantation forestry. Wood demand however is increasing and expected to continually increase as population is increasing with time and wood utilization getting diversified. All these contribute to the necessity to greatly increase forest productivity so as to meet national wood demand. One way to increase forestry productivity is through genetic improvement (Araujo, 1980).

This study intends to investigate the potential to boost forestry productivity by contributing to the knowledge regarding the best seed sources through evaluation of provenance trials of main and promising afforestation species in the country. The species include *Eucalyptus saligna, E. tereticornis, E. urophylla, Grevillea robusta, Pinus caribaea, P. kesiya, P. maximinoi, P. patula* and *P. tecunumanii.*

Apart from these species to be considered major or potential for afforestation in Rwanda, most of them are planted in the tropics and subtropics as reported by Eldridge *et al.* (1994) for *Eucalyptus* species, Burley (1976) for the pines (*P. caribaea, P. kesiya and P. patula*) and Harwood (1989) for *G. robusta.*

Objectives of this Research

- To assess the potential for increased timber production through geographic seed source introductions of relevant species, and
- To investigate the extent of genetic variation and age-age correlations in major reforestation species in the country and to establish a basis for future tree breeding activities.

2. LITERATURE REVIEW

2.1. Breeding strategies and the role of species and provenance introduction in a tree breeding programme

A breeding strategy is an overview or philosophy of the management of genetic improvement of a tree species used in man-made forests (Van Wyk, 1997). Tree breeding is a costly activity and care must be taken to avoid losses that may occur when unclear strategy is followed to achieve certain goals. Tree improvement may be more difficult to justify economically when forests are regenerated naturally, and the basic facts remain, that all forest management activities can profit from using tree improvement concepts (Zobel and Talbert, 1984).

Several authors have described factors to consider in developing a tree breeding strategy (Burdon and Shelbourne, 1972; Libby, 1973; Fowler, 1976). Genetic improvement programmes may vary considerably in design and intensity depending on species biology, organizational goals, forest management intensity and economic considerations (White, 1987). Examples of a tree breeding strategy in use include: a multiple population breeding strategy used in Zimbabwe (Barnes, 1984) and nucleus breeding (Cotterill *et al.,* 1989). An effective breeding strategy is based on both sound genetic theory as well as the implementation of the proper procedures (McKinley and Van Buijtenen, 1998).

Any tree breeding strategy should have its specific management objectives and always aim at achieving these at lowest possible cost for the highest genetic gains and within shortest possible time. It has to focus on both the operational (production) as well as developmental (research/breeding) phases (Zobel and Talbert, 1984) and if possible the two can be started at the same time (Van Wyk, 1997). The operational programme aims at making quick economic gains in terms of quantity and quality of the product while the developmental programme intends to broaden the genetic base and improve the breeding population at the same time.

Principles of a breeding strategy are outlined by Eldridge *et al* (1994) and Zobel and Talbert (1984). They consider several factors in common. First, they emphasize on the objectives of the

strategy, where the products needed and the urgency to produce them must be determined. Second, biological factors need be known and practical. Third, whether species, seed sources within species are known, and available and fourth, whether these match with the intended range of site conditions and with community expectations, fifth, whether financial resources are available and commitment to support the programme over a long term, with skilled personnel to carry out the programme so that its objectives are achieved. Lastly, the alternative breeding strategies and their biological and silvicultural practicability, with each strategy showing its expected gain in chosen traits in a specified period of time, should be available.

As pointed out, tree breeding programmes involve expenditure of considerable effort and money. Intensive breeding therefore is usually confined to species that are planted commercially on a large scale so as to justify the expenditure. Theoretically all traits can be improved genetically through breeding and the possibility of obtaining improvement in a specific trait varies considerably among species, and only becomes known after being studied (Wright, 1976).

Since geographic variation exists, and the differences among the races may be several times as large as the improvement expected from one or two generations of selective breeding, it would be wise to first study the geographic variation in a species and delay intensive selective breeding until the best geographic sources are identified (Wright, 1976). Geographic sources as well as individual tree variation are important in deciding whether to do selection. Seed collected from several trees in each of many stands scattered over a large area and seedlings kept separately by both parent and stand of origin give varied results in most cases. In some cases, differences among offspring of trees in the same stand are large, and those among the offspring of different trees in the same stand are small, leading to the conclusion that selection and crossing of individual trees is unnecessary (Wright, 1976). In cases where the variation between the offspring of the individual trees is considerable, intensive breeding work is justified.

A concern of research testing in provenance trials is to determine whether a good genotype selected in one environment will also perform well in another environment relative to other genotypes in a test (Ladrach, 1998). This genotype by environment interaction means that the relative performances of clones, families, provenances or species differ when they are grown in

different environments (Zobel and Talbert, 1984). Since both genotype and environment affect the performance of a given tree as observed in different traits, the genetic improvement obtained through breeding can be added to the one obtained through silvicultural treatment. As there is a mutual reinforcement between genetic and cultural improvements, a genetically faster growing species may justify more intensive culture, which in turn will justify more planting (Wright, 1976). Major gains can be made using location specific sources when limits are known and this is especially true for extreme sites where tolerances to unique or extreme conditions are critical (Ladrach, 1998).

2.2. Genecological studies of exotics and plantation forestry in the tropics

2.2.1. Species and provenance concept

It is well known that different geographic origins of seed used for planting a particular tree species can lead to substantial differences in growth, form and health of the resulting plantations. The differences within a species can be so large that one lot of seed will result in successful, profitable plantations and another in complete failure (Eldridge *et al.,* 1984). It is therefore of prime importance to know the place of origin of seed and obtain the seed from the best source.

The use of genetically-based, geographic variation is the first step in tree breeding when assembling a suitable base population for future generations of selection, crossing and genetic improvement. The concept of provenance implies that genetic patterns of variation are associated closely with the ecological conditions in which the species evolved (Turnbull and Griffin, 1986). The recognition of such patterns of variation is made through genecological studies, mainly of phenotypic variation in natural forests (Eldridge *et al.*, 1994). Little is known about genetic variability of tropical hardwood populations and it is common to observe an obvious gap between listing of species for reforestation and availability of data on performance of such species under different climatic conditions (Midgley, 1983).

Tropical plantations are mainly made by exotic species. Reasons for this include little knowledge available concerning the silviculture and management of indigenous species; failure of local species to provide desirable products, easiness of exotic tree species to establish on modified or

degraded sites (Wright, 1976; Zobel *et al.*, 1987), quicker rotations and hence quicker returns of exotic compared to indigenous species. Reforestation in the past has been done either using species whose seed is readily available or the known species through experience. Some-times seed used were of unknown origins or collected from very small plantations/populations with high chances of having limited genetic base.

Although given little attention, using trees of restricted genetic potential is a limiting factor when dealing with exotic tree species for reforestation purposes. Often such species fail to fully exploit the productive potential of the new site, resulting in limited productivity. Productivity can therefore be improved through scientific selection of species and provenance (Evans, 1982). An economic increase of 27-45% in internal rate of return on investment in China is reported resulting from correct selection of provenances (McKinley, 1991).

2.2.1.1. Species introduction

Often, the information on the requirements of the species or on characteristics of the sites, or both, is lacking (Hughes and Willan, 1976, Willan, 1980). In such cases, embarking on afforestation programmes without carefully planned and executed experimental procedures has often led to costly failures. The choice of species to use involves the extrapolation of information from elsewhere. Climatic and ecological matching of a new site and the original habitat of a new species is rarely enough since it cannot reveal the adaptability of the species to new site conditions or its ability to grow satisfactorily on a range of sites (Willan, 1980). Recent developments in interpolating climatic data have greatly improved the ability to assess the potential of sites in different regions, countries or throughout the whole world (Turnbull and Booth, 1994). Several authors have summarized new methods to predict where and how well different species and provenances may grow in different environments. These include Booth (1985, 1991), Booth and Jovanovich (1987), Booth *et al.*, 1987, 1989).

The traditional way to acquire enough information on adaptability of a species to a new site is to test a number of species usually in small plots on representative sites within the area of reforestation programmes. Different authors outline species trial phases including: FAO (1975); Hughes and Willan (1976); Wright (1976); Willan (1980); Evans (1982); Burley and Plumptre (1984). The stages are: species elimination phase, species testing phase and species proving phase.

The species elimination phase is a mass screening of large numbers of possible species in small plots for a short period to determine survival and promise of reasonable growth. The duration of such trials is reported to be 0.1 to 0.2 times the rotation age (Burley *et al.*, 1976; Willan, 1980).

The species-testing phase, also known as species refinement (Evans, 1982) and species performance stage (Leuchars, 1965), is assigned for the critical testing of, or comparison of reduced number of promising species in large plots for longer periods. The duration of the trials is reported to be 0.25 to 0.5 times rotation age (Burley et al.1976, Willan, 1980). The species-proving phase, also known as industrial scale trials (Evans, 1992) or management trials and the crop performance phase (Lauchers, 1965) are designed to confirm, under normal plantation conditions, the superiority of a few probable species.

2.2.1.2. Provenance research

The term provenance has been defined by several authors: Callahan (1964); Roche (1971); Jones and Burley (1973); Styles (1976); Wright (1976) and Zobel and Talbert (1984). In a comprehensive review of the concept of provenance and its importance in forestry, Turnbull and Griffin (1986) considered the definitions and explanations of current usage of the term provenance by such organisations as the society of American Foresters and the Organization for Economic Cooperation and Development (OECD). They noted that the several published definitions were somewhat contradictory and were loosely used in forestry practice but

nevertheless, "this concept is of major practical and economic significance." They concluded that it is incumbent upon the user to provide the appropriate definition.

For the purpose of the present study, provenance refers to geographical area or region, covering a species natural range, or where a species has developed into a landrace, from which seed or propagule sample has been collected and used to establish a plantation in a new environment where the species is an exotic. A landrace is defined as a population of individuals that has become adapted to a specific environment in which it has been planted (Zobel and Talbert, 1984). To be identified as a landrace, the original source must be among the best available; must have a broad genetic base including some of the best individuals; selection in the past, both natural and artificial, must have been intense enough to genetically change the population towards a better adaptation; and the plantation must be large enough to allow intense selection in the future (Zobel and Talbert, 1984). The "provenances" and landraces are mostly referred to as "seed sources" and "local (seed) sources" respectively in this study to avoid confusion.

In selecting provenances three stages similar to those of species introduction trials apply to provenance testing for species with a wide natural distribution: a range wide provenance sampling phase, a restricted provenance sampling phase and a provenance proving phase (Willan, 1980). Since these phases usually apply to species considered likely or promising, plot size and time scale may exceed those utilized for the comparable phases of species trials.

Provenance testing is done for two purposes (Wright 1976). The first is to uncover evolutionary trends and relate them to factors of the environments in which the trees evolved; second and very practical one is to screen the naturally available genetic variation and to choose the best available types for reforestation or further breeding work. It is particularly important therefore to do provenance testing prior to embarking on intensive breeding work when dealing with exotic species. In some species, there are 4:1 differences or more in growth rate and corresponding large differences in other traits between different races of the same species. An example is that of *Eucalyptus camaldulensis* in Nigeria and in Israel. The volume yields in the best and worst provenances were in the ratio of 3:1 at the age of six years at Afaka in Nigeria (Lacaze, 1970)

and 8:1 at 10 years at Gan Hadar (Israel)(FAO, 1989). A breeder must therefore be sure he has the best race before starting crossing work and seed orchard establishment (Wright, 1976).

Genetic gains from growing exotics are determined by the quality of the geographic race or the seed source used (Squillace, 1966). Several other authors emphasize the importance of provenance testing prior to the establishment of an exotic tree species for better results. These include: Yeatman (1976); Eldridge (1978) and Zobel *et al.* (1987). Plantations in the developing countries often are failures due to the lack of research on provenances (Steinberg, 1983).

Genetic gains in addition to those from using the best provenances are possible by selecting the best individuals within provenances because of the very large variability in forest trees (Wood and Greaves, 1977; Guries 1984). An understanding of the pattern and the degree of genetic variability within species is essential for sound management and conservation of genetic resources as well as for developing appropriate tree improvement strategies in plantation forestry.

Genetic variation studies, particularly provenance trials are commonly restricted to commercially well-known species mainly used for timber and other wood based products such as paper, plywood, chipboard, etc. Due to their well-known management practice and silviculture as well as wood properties, softwood species are more extensively studied than tropical hardwoods, exception probably being *Eucalyptus* species. There are many books and publications on provenance research results for different exotics in different locations. Summary publications such as those by Burley and Nikles (1973); Dorman (1975) and Nikles *et al.* (1978) list many study results and describe the techniques used in provenance breeding and testing. Many other authors including Gerhold (1959); Langlet (1959); Mergen and Worrall (1965); Steinbeck (1965; 1966); Jenkinson (1966); Schultz (1969); Lee (1969); Wright (1969); Mitchell (1970); Rahman (1970); Lines and Mitchell (1970); Cech *et al.* (1974); Bunvong (1981); Rubin *et al.* (1974); Prus-Glowacki and Szweykowski (1977) and Krzakowa (1980; 1982); Mejnartowicz and Bergman (1984); Geng (1989); Kuser *et al.* (1989); Jiang *et al.* (1989); Falkenhagen (1991); Mekic and Larsen (1991); Woolaston *et al.* (1991); Raymond *et al.* (1992); King *et al.* (1992); Sassidharan *et al.* (1992); Barnes, *et al.* (1992); Ottegbeye and Samarawira (1992); Phillips and

Aradhya (1993); Lin and Zsuffa (1993); Li *et al.* (1993); Park and Kassaby (1993) and Anderson *et al.* (1994) studied and report the existence of genetic variation among and within provenances and families for different traits in different tree species.

Further and specific information as published by different authors on provenance variation is given in Tables 2.1 and 2.2.

Table 2.1: Interpopulation genetic variation of softwood species used as exotics in different countries.

Species	Country	Author(s)
Laryx spp.	Denmark	Keiding and Oresen (1965)
Cupressus lusitanica	East Africa	Dyson and Raunio (1971)
P. caribaea	Congo	Chaperon (1977)
P. caribaea	Brazil	Kageyama *et al.* (1977)
P. caribaea	Indonesia	Long and Dykstra (1983)
P. merkusii	Thailand	Pousujja (1984)
P. patula	Zimbabwe	Barnes (1973)
P. patula	Tanzania	Nshubemuki, *et al.* (1996)
P. patula	S. Africa	Denison (1973)
P. patula	Brazil	Kageyama *et al.* (1977)
Pinus radiata	New Zealand	Bannister (1969)
P. radiata	Australia	Eldridge (1974)
P. rigida	Korea	Ham *et al* (1984)
P. sylvestris	Holland	Squillace, *et al.* (1975)
Picea sitchensis	Great Britain	Burley (1966)

2.2.1.3. Experimental design for species, provenance and progeny testing

The optimum design is likely to vary with traits measured and the specific purposes of each experiment. The breeder must obviously compromise among the multiple objectives and construct a single or a few designs (Namkoong, 1984). One way to achieve this is to choose a single design, which is reasonably good for all objectives (Namkoong *et al.*, 1980). There are three main sources of error in provenance experiments. Firstly, errors due to site heterogeneity, secondly, that due to genetic differences between trees and thirdly, observer error at time of assessment (Barnes and Gibson, 1984). Proper experimental and genetic designs can minimise the first and the second errors respectively while the third error can be minimised by careful assessment procedures on selected traits (Barnes and Gibson, 1984). Spacing, plot size and shape, blocking arrangement and repetition over environments are the features of design that can be

varied depending on resources available and the objective of the experiment. Close spacing allows trials to be laid out in smaller areas.

Table 2.2: Interpopulation genetic variation of hardwoods used as exotics in different countries.

Species	Country	Author(s)
Acacia mangium	Philippines	Peterson and Havmoller (1984)
Calliandra calothyrsus	Rwanda	Gahamanyi (1989)
Castanea molissima	USA	Keys *et al.*, (1977)
Cedrela odorata	Ivory Coast	Britwum (1977)
C. odororata	Uganda	Britwum (1977)
C. odororata	Nigeria	Britwum (1977)
C. odororata	Nigeria	Egenti (1977)
C. odororata	Tanzania	Malimbwi (1977)
Eucalyptus grandis	Florida	Van Wyk (1976)
Eucalyptus spp.	Several	Boland (1978)
E. camaldulensis	Israel	Grunwald and Karschon (1983)
Eucalyptus camaldulensis	South Africa	Darrow (1983)
E. camaldulensis	Madagascar	Ranaivoson (1989)
E. camaldulensis	South Africa	Darrow and Roeder (1983)
E. camaldulensis	Madagascar	Ratsohaeilala (1987)
E. camaldulensis	Italy	Sesbou and Nepveu (1978)
E. camaldulensis	Pakistan	Siddiqui (1979)
E. camaldulensis	India	Ghosh *et al.* (1977)
E. camaldulensis	Brazil	Moura (1986)
E. camaldulensis	Brazil	Moura *et al.* (1987)
E. camaldulensis	Sri Lanka	Vivekanandan (1978)
E camaldulensis	Israel	Karschon (1966, 1967)
E .cloeziana	Zimbabwe	Hughes (1988)
E. cloeziana	Tanzania	Madoffe and Maghembe (1988)
E. deglupta	Australia	Jahnke *et al.* (1983)
E. deglupta	Papua New Guinea	Davidson (1983)
E. deglupta	Puerto Rico	Whitmore (1973, 1983)
E. deglupta	Puerto Rico	Whitmore and Marcia (1975)
E. delegatensis	Sao Paulo	Long and Dykstra (1983)
E. delegatensis	Australia	Abbott and Pederick (1984)
E. fastigata	New Zealand	Wilcox (1982)
E. grandis and E. saligna	Australia	Moran *et al.* (1990)
E grandis	South Africa	Van Wyk (1883)
E. saligna	Rwanda	ISAR (1997)
E. saligna and E. grandis	South Africa	Roeder (1980)
E. tereticornis	Rwanda	ISAR (1997)
E. tereticornis	Hawaii	Skolmen (1986)
E. tereticornis	Nigeria	Ottegbeye (1990)
E. urophylla	Rwanda	ISAR (1997)
E. urophylla	India	Chaturvedi *et al.* (1989)
E. urophylla	Ivory Coast	Diabete (1978)
E. urophylla	Ivory Coast	Wencelius (1983)
E. urophylla	Malawi	Ngulube (1989)
E. urophylla	China	Zhou and Bhai (1989)
E. urophylla	China	Suseno *et al.* (1985)
E. urophylla	Indonesia	White (1989)

Also greater plot and block uniformity can be achieved and maintenance costs are reduced. It also makes an early assessment of maximum basal area possible and it is possible that through early crown closure, competitive ability might be assessed early (Franklin, 1979). Between tree spacing needs to be larger in provenance than in species elimination trials since the former should have to run at least half the length of the expected rotation (Eldridge *et al.*, 1994). The disadvantages of smaller spacing are that if the trial is to be more than very short term, complex decisions about thinning the trial will have to be made sooner, trait assessment and preservation of trees for breeding purposes may be prejudiced (Barnes and Gibson, 1984). For provenance trials at wider spacing over half rotation age, and where large differences between provenances are expected, a minimum plot size of 6 x 6 (36) trees is recommended, with the inner 4 x 4 (16) trees assessed (Eldridge *et al.*, 1994, Barnes and Gibson, 1984). Square spacing is usual with plant spacing varying from one to four metres, but if there is a particular reason for a rectangular spacing, e.g. equipment used for cultivation, it does not affect the results to have up to double spacing in one direction (Daniels and Schutz, 1975; Bredenkamp, 1982).

The blocking and the replication of the experiments over sites is dependent on several factors. These include the scale of the expected differences between provenances, number of provenances to be tested, the heterogeneity of the trial sites and the security of the experiment against damage or loss at the individual tree, block or whole experiment level (Barnes and Gibson, 1984). A minimum of four and preferably five or more replications per site is recommended (Eldridge *et al.*, 1994). The experimental layout varies depending on trial objective, size and expected risks among other things. Lost plots cause little problems in simple designs. For this reason, complete randomisation (without blocks) and randomised complete block designs (RCB) are preferable to the more complex designs when missing whole treatments (seedlots) are expected due to death or very slow growth of some seedlots (Eldridge *et al.*, 1994). Four replicates is the absolute minimum for well-conducted trials with good survival on less variable sites (Eldridge, *et al.*, 1994). The RCB designs are mostly used in forestry due to their simplicity but are less precise and when a number of seedlots to be compared is large, incomplete block designs are always recommended, although these require sufficient statistical and computing skills (Eldridge *et al.*, 1994). The use of incomplete block designs such as alpha design (John, 1987) greatly increases

statistical efficiency and the chance of detecting, with confidence, the differences between seedlots (Eldridge *et al.*, 1994).

Plot shape in progeny testing varies from row to square or rectangular patterns, and the smaller the plots, the greater the number of replicates planted (Eldridge *et al.*, 1994). In progeny testing, plot size is often smaller than in provenance testing, and breeders normally aim at 20-60 trees per family depending on the variability of the experimental site. Twenty trees per family are usually adequate to obtain reliable estimates of family characteristics in *Pinus radiata* (Cotterill, 1984). The designs with small plots and large numbers of replicates may give good statistical precision but are more difficult to establish because the identity of each seedling must be maintained. Row plots of six trees (1 x 6) with six to 10 replicates are usually used in progeny testing (Eldridge *et al.*, 1994).

2.2.2. Genetic variation and inheritance in tree growth traits

Considerable variation exists between populations and individuals and they may be attributed to genetic and environmental forces and their interactions. Variation studies are important whenever selection is the basis of genetic improvement (Beddel, 1989). Genetic gains in addition to those from using the best provenance are possible by selecting the best individuals within provenances because of the very large variability within forest tree species (Wood and Greaves, 1977).

An important factor related to tree improvement is to understand the relationship among different characteristics of the tree. Fortunately, most of the important characteristics in forestry are partially or almost totally genetically unrelated. It is therefore possible to have fast growing trees that are straight or crooked or straight trees that have small branches or large branches because the characteristics of growth rate, stem form and branch size are not genetically closely related (Zobel *et al.*, 1987).

The lack of correlation of adaptive versus economically important form and growth characteristics is of high importance to one growing exotics. This makes it possible to breed intensively for broadening the adaptive genetic base (against insects, diseases, adverse sites or

adverse weather) and at the same time breed strongly for greater uniformity in tree form and wood quality or other properties (Zobel and Talbert, 1984). This is extremely important in exotic forestry since it makes it possible to develop well-adapted strains of trees that also have desired economic characteristics. An example to this is that by Wilcox (1982) where he reports the absence of any major adverse correlation of frost hardiness and growth rate for *Eucalyptus fastigata*. It is often claimed that for *Eucalyptus*, faster growers are more sensitive to cold damage; when this occurs, the faster growers tend to be more forked as a result of frost damage.

2.2.3. Heritability in forestry

Heritability is defined as the portion of total variation caused by genetic influence alone (Tootil, 1990). Williams and Matheson (1994) define heritability as the usable (or additive) genetic variance for a trait in a population expressed as a proportion of the phenotypic variance. The phenotypic variance is usually estimated as the sum of the seed lot variance components (usually estimated from families) - the plots level variance component (σ_p^2) and the trees level variance (σ_t^2) (Williams and Matheson (1994). Where the analysis has been carried out on plot means, the residual variance contains both plots level and trees level variance components. Heritability is the degree to which variability in a trait between trees is influenced by genetic factors and is transmitted from parent to offspring (Shelbourne, 1969). Heritabilities of less than 0.1 are considered low, between 0.1 and 0.3 intermediate and above 0.3 high (Cotterill and Dean, 1990). Open pollinated families are derived from seed collected from individual seed parents in which pollination is uncontrolled. The assumption here is that each seedling in such a seed lot has the same mother tree and a different and unrelated pollen parent. In this case, the coefficient of relatedness (r) of each seedling with each other seedling in the same family is ¼ and they are strictly half sibs (Williams and Matheson, 1994). This however rarely occurs, especially in natural populations in which there may be some family structure. There are seedlings likely to be with the same or related fathers, and perhaps there will be seedlings resulting from self-pollination. In such cases, the coefficient of relatedness is likely to be greater than 1/4 (Williams and Matheson, 1994). The average coefficient for open pollinated seed from unrelated pines was estimated to be 1/3 (Squillace, 1974). Due to greater propensity for self-pollination in the

eucalypts in natural populations, the coefficient of relatedness is recommended to be 1/2.5 (Williams and Matheson, 1994) and 1/3 for *E. grandis* (Snedden *et al.*, 2000).

Different authors who worked on different tree species in different locations have published heritability of growth and stem straightness, branch size and angle, etc. Some results on test species are shown in Table 2.3.

Table 2.3: Heritability values in different traits of softwood and hardwood species used as exotics in different countries.

Species	Heritability	Trait	Country	Author(s)
Pinus caribaea	0.04-0.53	Height	Puerto Rico	Ledig and Whitmore (1981)
P. caribaea	0.11	Volume	Puerto Rico	Ledig and Whitmore (1981)
P. caribaea	0.53	Bark thickness	Puerto Rico	Ledig and Whitmore (1981)
P. caribaea	0.17	Fox tailing	Puerto Rico	Ledig and Whitmore (1981)
P. caribaea	0.36	Height	Brazil	Kageyama (1984)
P. caribaea	0.12	Height	Indonesia	Long and Dykstra (1983)
P. caribaea	0.40-0.75	Fox tailing	Australia	Sato and Brune (1983)
P. caribaea	0.06-0.70	Height	Australia	Sato and Brune (1983)
P. caribaea	0.13-0.71	Diameter	Australia	Sato and Brune (1983)
P. caribaea	0.86	Height	Australia	Bridgen and Williams (1984)
P. caribaea	0.89	Diameter	Australia	Bridgen and Williams (1984)
P. caribaea	0.86	Volume	Australia	Bridgen and Williams (1984)
P. patula	0.24	Stem straightness	Colombia	Lambeth and Ladrach (1991)
P. patula	0.46	Bole forking	Australia	Lambeth and Ladrach (1991)
P. patula	0.35	Bark vol.	Australia	Lambeth and Ladrach (1991)
P. patula	0.38	Height and volume	Australia	Lambeth and Ladrach (1991)
E. tereticornis	0.26	Height	India	Kedharnath and Vakshasya (1977)
E. tereticornis	0.25	Diameter	India	Kedharnath and Vakshasya (1977)

There are no uniform trends in heritability for diameter and height of different species. Reports by different authors as cited by Harap and Soerianegara (1977) indicate that in some species, heritability is higher in height than in diameter (Toda, 1958; 1959; 1961; Albez and Miller 1972; Suksileung *et al.*, 1975; Harap and Soerianegara, 1977). Others report higher heritabilities in diameter than in height (Sokai and Hatekayama, 1963, Sinues, 1973 and Djamhuri 1975). Whether there is a trend or not, what is most important is that heritability for the two parameters does exist and selection can lead to genetically based tree improvement. Several authors as cited by Wright (1976) worked on eastern and western white pines (*Pinus monticola*), Japanese red pine (*P. densiflora*), slash pine (*P. elliottii*), Monterey pine (*P. radiata*), Scotch pine (*P. sylvestris*), jack pine (*P. banksiana*), ponderosa pine (*P. ponderosa*) and loblolly pine (*P. taeda*)

in USA: Woessner (1965), Zobel *et al.* (1973), Zobel (1971), and Anon. (1970). They all report in common that the species indicate high heritabilities in growth traits and stem form characteristics. Martinson (1982) indicates that there are provenance differences in root characteristics, and this could certainly be utilized in selection and tree improvement.

2.2.4. Genetic variation and inheritance in wood properties

2.2.4.1. Wood density/specific gravity

Density refers to the mass of substance per unit volume. Specific gravity is the ratio of density of a material to the density of water, at its greatest density, which is at 4^0C. At this temperature, the density of water is 1000 kg/m^3. Of all physical properties of wood, density (or specific gravity) is the most important. The weight of a given volume of wood is generally an index of amount of cell wall substance present and of the volume comprised of air spaces. The amount of wood substance in a given piece is a reliable indicator of its strength properties, and to some extent, of its working and finishing characteristics. The air space indicates the amount of water it can absorb.

It is generally assumed that the quality of wood depends mainly on its density (Ishengoma and Nagoda, 1991). There is a close relationship between density and mechanical properties, dimensional changes with changes in moisture content below fibre saturation point, and the heat value of wood (Ishengoma and Nagoda, 1991). By influencing basic properties therefore, density influences the utility of wood. Genetic variation is caused by both genetic and environmental factors (Larson, 1973, Klem, 1984). They found that the genetic component of specific gravity variation is considerable compared to that attributable to environmental factors.

The rate of growth in general does not necessarily affect the specific gravity of wood. Any factor that alters the growth pattern of a tree however, may change its wood properties (Larson 1973; Zobel and Talbert, 1984). Negative correlation between specific gravity and growth rate in *Eucalyptus grandis* is reported in Madagascar (Ranaivoson, 1989). A similar observation was

made in *Pinus taeda* in Georgia (Stonecypher, 1966). A tendency towards higher specific gravity at higher altitudes and latitudes, localities with higher moisture deficits and climates where there is a pronounced dry season has been reported (Zobel, 1965; Polge and Kellen, 1968; Barnes *et al.*, 1977; Plumptre, 1984).

Specific gravity differences between provenances are in most cases non-significant if averaged over several sites and if they are, they normally only account for a small percentage of total variation. Within sites however, the differences can be quite large and highly significant (Zobel, 1965; Plumptre, 1984). Non-significant differences in specific gravity in *Eucalyptus grandis* were found between populations or locations in Kerala (India) (Bhat *et al.*, 1990). Tree to tree variation in specific gravity of mature wood is much greater than variation between regions, or sites or clones (Zobel and McElwee, 1958; Goggans, 1961) and usually very high (Zobel *et al.*, 1987). The individual tree differences create difficulties in obtaining clear provenance patterns, but make it ideal for improving wood through breeding since much of the variation is genetic in nature (Smith, 1966).

As should be clearly understood, wood variation among species within genera can be very large, but even this is not always appreciated. An example of species differences cited for *Eucalyptus* by Higgins (1985), the mature wood density of different species ranged from 300 to nearly 1000 kg/m^3.

Although wood properties of species used as exotics are generally well known, and usually thoroughly studied in their indigenous habitat, the information available is sometimes incorrect may even be misleading relative to wood of the same geographic source when grown in a new environment (Zobel *et al.*, 1987). It is therefore a major error to think that, because wood of a native species is good, it will be good as an exotic in a different environment (Zobel *ET AL.*, 1983). Change from the native habitat to the strange habitat affected wood of a number of species including *Larix decidua*, *Tsuga heterophylla*, *Eucalyptus globulus* and *E. saligna (*Wright, 1962). The need to test wood before establishing seed orchards for seed production was emphasized by Thompson and Nelson (1984).

Studies on temperate hardwoods showed a range of 0.2 to 0.7 for specific gravity (Gabriel, 1956; Harris, 1965; Zobel 1965). A strong inheritance for specific gravity in crosses between certain spp. of *Eucalyptus* is reported with the hybrid being intermediate between the parents (Pryor *et al.*, 1956). Since trees of same species as well as provenances vary in specific gravity, and since specific gravity is heritable, individual and provenance selection can be used to improve this trait in exotic forestry.

2.2.4.2. Fibre length

Except for wood density, the inheritance of fibre length has been the most studied wood property in the hardwoods because it is considered to be the limiting factor in their use (Zobel and Jackson, 1995). The fibres of most hardwoods are short, making them useful for certain products and undesirable for others. For example, it is considered to be the most important characteristic (together with wall thickness) for making high quality ground wood in the eucalypts (Zobel and Jackson, 1995). Fibre length has proven to be strongly inherited but the value of an improvement in length is usually questioned, since most fibres are short and rarely longer than 1 mm (Zobel and Jackson, 1995).

Fibre length has not been shown to influence solid wood properties however, it is an important characteristic determining paper strength and therefore important in plantation forestry (Zobel, 1965; Metcalfe and Chalk, 1983; Bhat *et al.*, 1990). Klem (1984) reports that knotty wood tends to have shorter fibres, which are unwanted in pulpwood. Longer fibres therefore are better for pulp and paper industry.

Geographic variation as well as tree-to-tree variation has been reported in fibre length within stands of some species. Different authors in different species report variation in fibre length differently. Some authors including Meyer-Uhlenreid (1959); Zobel (1965); Smith (1966) and Taylor (1973) report that no such differences exist. Others report large variation in the trait among individual families and individual trees when grown under similar conditions (Taylor,

1965; Akachuru, 1984). It may therefore be true that there is no general trend in variation in this species since the different authors worked with different species in different places.

Bhat *et al.*(1990) reported longer fibres on a site where growth rate was higher in *Eucalyptus* but no consistent relationship was found between fibre length and height or diameter. Fibre length is reported to increase with age (Bamber *et al.*, 1969; Bamber, 1978; Bhat *et al.*, 1990) but trees with either shorter or longer fibres than average retain this relative position, as they grow older (Goggans, 1961). Fibre lengths of trees of the same species in a population show genetic variation. Heritabilities of up to 0.86 were reported for Poplars by van Buijtenen *et al.*, 1962).

Geographic differences from varied test sites were reported to be due to site effects and not true genetic differences related to the place of origin of the seed in *Liriodendron tulipifera* (Thorbjornsen, 1961).

2.2.4.3. Other wood properties

Variation in wood characteristics other than specific gravity and fibre length has been comparatively less studied. Anderson *et al.* (1994) report geographic variation in gum composition of *Leucaena diversifolia* and *L. leucocephala* with the former being more variable. Metcalfe and Chalk (1983) report geographic variation in wood characteristics such as grain, chemical content and durability.

Large variation is said to exist in wood strength properties between trees of *Pinus caribaea* (Plumptre, 1984). Strength properties are said to vary more than density (Bower *et al.*, 1976). Lowest compression strength in studies on *P. caribaea* was found to be 40 % of the highest value (Fahnestock and Garratt, 1938).

2.2.5. Intrapopulation genetic variation in forest trees

Forest trees are subject to evolutionary forces that differentially affect the distribution of genetic variation within and among their populations. Natural selection favours adaptation to environmental gradients of patchily distributed habitat variation (Hamrick and Nason, 2000). Factors such as small population size and inbreeding reduce within population genetic variations but further contribute to genetic variation among populations. Although the evolution of population genetic structure is a result of complex interaction of natural selection, drift and gene flow, tree species with high rates of gene flow should have relatively more genetic variation distributed within and less among populations than species with more limited gene movements (Hamrick and Nason, 2000).

Factors influencing the amount of geographic variability are classified by Wright (1976) as, first, the size of a species range, second, amount of environmental diversity and third, the extent of range discontinuities. Rapid and large-scale changes in the extent and integrity of forest ecosystems following deforestation due to human activities and population pressure have resulted in fragmented forests, often with little physical, and probably limited functional resemblance to the original one (Young and Boyle, 2000).

Changes in the species composition of forest communities have been observed to accompany forest fragmentation, especially at newly created edges (Ranney *et al.*, 1981; Young and Mitchell, 1993). These primarily reflect ecological responses to fragmentation due to changes in disturbance regimes or microclimate and represent the genetic response at the macro scale (Young and Boyle; 2000).

These processes will, more directly, at intraspecific level, effect changes in population size, and isolation associated with reduction in forest cover, that will affect genetic processes such as mating, gene flow and selection that determines the level of genetic diversity maintained within plant species (Belington, 1991; Ledig, 1992; Young *et al.*, 1999).

Just as comparative provenance tests are used to determine how much of the genetic variation between materials of diverse origins is inherited and how much is due to the conditions under which they are growing, so are progeny tests used to demonstrate inherent differences between individual trees within a given population. In forest trees, variability is quite important (Zobel *et al.*, 1960) and the higher the variability of a population, the better the chances to select individuals with desirable characteristics (Cossalter, 1989).

2.2.6. Juvenile-mature and trait-trait correlation in growth and wood quality traits

Juvenile-mature (age-age) and trait-trait correlations are expressed as genotypic or phenotypic coefficients between pairs of data sets taken at different ages or different traits. Significant correlations between young or juvenile and mature growth may allow for prediction of volume or yield at rotation age. Likewise, significant correlation between traits may allow for selection for a trait, which is difficult to measure by making use of a related trait, which can be assessed more easily. Genetic correlation is an expression of correlated response to selection. If one trait is selected, what response is there in another trait? It is based on the estimates of genetic covariance between traits from a progeny test (Eldridge *et al.*, 1994). Phenotypic correlations, which include genetic and environmental components, are simply calculated from the corresponding measurements of two traits for each of several trees. Genetic correlation is much more important to the breeder as it is the correlation of the breeding value (Faulkner, 1998). Breeding value is the value of an individual judged by the mean value of its progeny (Eldridge *et al.*, 1994).

Apart from height, diameter, stem straightness and branching characteristics, assessment of progeny tests also includes wood properties and timber defects. Many of the wood and growth characteristics are related, and once the genetic correlations among different traits are determined (from progeny tests), assessment procedures could be simplified or reduced by making use of favourably correlated responses between pairs of traits (Eldridge *et al.*, 1994). Simple but reliable procedures are best for assessing offspring. For instance, splitting of eucalypt logs is caused by a variety of factors, not all of which are yet known. However, log end splitting itself is relatively easy to assess in the field three days after the tree is felled (Van Wyk and Hodgson, 1983).

Correlation between characters is an important factor to consider in any selection and can be studied both at individual or provenance level. In provenance evaluation and selection, correlation at provenance level, provenance means are most important (Keiding *et al.*, 1984) and these are phenotypic correlations. The extent to which the phenotypic correlation reflects the genetic correlation at provenance level will depend on the reliability of the phenotypic provenance means (provenance mean h^2). If they are high for the recorded character, the phenotypic correlations are close to the genetic ones otherwise they often underestimate the genetic correlation (Keiding *et al.*, 1984).

Genetic parameters have been reported to change with age by a number of authors in different species. These include Clausen (1982) for *Juglans nigra* and *Fraxinus americana*; Wakeley, (1971) and La Farge (1972) for *Pinus. taeda*; Steinhoff (1974) and Namkoong and Cockle (1976) for *P. ponderosa*; Namkoong *et al.*, (1972) for *Pseudotsuga menziesii*, Squillace and Gansel (1974) for *Pinus elliottii*; Samuel and Johnson (1976) for *Picea sitchensis*; Schultz (1983) for *Liquidambar styraciflua*; Rink (1984) for *Juglans nigra* and Wilkinson (1973) for various hybrids of Poplars.

Juvenile-mature correlation for volume and other characteristics in individual forest trees is nearly always poor except for very short rotations (Zobel *et al.*, 1987). Ranking of juvenile mature correlations for *Pinus oocarpa* in Kenya indicated its variability in the first four years, but in the fifth year, a clear picture emerged regarding provenance superiority (Chagala and Gibson, 1984).

Premature provenance selection may lead to mistakes due to poor juvenile mature-correlations (Zobel and Talbert, 1984). To get reasonable juvenile-mature correlations (especially for growth related characteristics) a period of half rotation age is required (Zobel and Talbert, 1984). It is recommended to assess tropical pines at the age of eight years (Barnes and Gibson, 1984) and at ten years (Liegel, 1984).

2.3. General distribution of the genera *Eucalyptus, Grevillea* and *Pinus*

2.3.1. The genus *Eucalyptus* (Myrtaceae)

The genus *Eucalyptus* l'Heritier is one of large size and great complexity. Different authors give different figures regarding the number of species in the genus. 500 spp and 138 varieties are reported by Blakeley (1955); Blakeley, 1965; Pryor and Johnson, 1971; Chippendale, 1976) and 600 spp. by Florence (1996) while Brooker and Keinig, (1994) report 800 spp. With but few exceptions, these taxa are all endemic in Australia the majority occurring, south of the Tropic of Capricorn (Poynton, 1979). Several however are indigenous to New Guinea or to certain Islands in the Indonesian Archipelago, including Timor, Wetar, Flores and the Lesser Sunda Islands, while *E. deglupta* follows the line of active volcanoes which stretches from New lreland, New Britain and New Guinea through Sulawesi (Celebes) and the Moluccas, to Mindanao in the Philippines (Jacobs, 1976).

The eucalypts are adapted to a wide range of climates since they naturally occur over a wide geographic distribution. They naturally occur from Latitude 7^0N to $43^0$39' S (Jacobs, 1976) and from sea level to about 1800 m.

2.3.2. The genus *Grevillea* (Proteaceae)

Grevillea is a name given to the largest sub-family of Proteaceae, the *Grevilleoidea,* which has about 40 genera (Makinson and Boland, 1992). This sub-family represents the Southern Hemisphere distribution of the family as a whole, with the majority of the genera found exclusively in Australia, some representatives are found in South-East Asia, South America, and in some Islands in the Pacific. Two monotypic genera are endemic to Southern Africa and Madagascar. *Grevillea* is one of only three genera in the tribe *Grevilleeae*, the other two being *Hakea* Schrad. and *Fischia* Warb. both endemic to Australia/south west Pacific region (Makinson and Boland, 1992).

Grevillea is a successful woody genus. This is because it has radiated to occupy a relatively wide range of habitats. The ancestral *Grevillea* was probably a forest tree, but nowadays species range from shrubs of alpine swamps to tropical rain forest trees, the greatest number being shrubs of sclerophyllous communities on well drained, phosphorus-deficient soils in temperate south-eastern and south-western Australia (Makinson and Boland, 1992).

2.3.3. The genus *Pinus* (Pinaceae)

All pines comprising approximately 100 species belong to the genus *Pinus* (Mirov, 1967) and there are a great many named hybrids, varieties, forms and cultivars (Loock, 1950; Dallimore and Jackson, 1966). The genus is well represented from the Arctic Circle to the subtropics, occurring in Europe, North Africa, Asia, Asia Minor, Malaysia, Oceania and North and Central America (Dallimore and Jackson, 1966; Mirov, 1967). It is the most widely spread of the Pinaceae, extending across the Northern Hemisphere roughly between latitudes 15^0 N and 70^0 N in North America and Eurasia (Styles and Faljon, 1997).

P. merkusii has a rather more tropical distribution (most southerly distribution) and crosses the equator at the southern extremity of its range in Indonesia (Critchfield and Little, 1966). In the New World, *P. caribaea* and other species penetrate south to the Caribbean region (Poynton, 1977). Altitudinal distribution ranges from sea level for *P. caribaea* var. *bahamensis* in the Bahamas to 4000 m for *P. hartwegii* in Mexico (Styles and Faljon, 1997).

2.4. Distribution, site conditions and characteristics of test species

2.4.1. *Eucalyptus saligna*

E. saligna Smith (Sydney red gum) is fairly widely distributed in the coastal belts of Central and Northern New South Wales and Southern Queensland as well as along the adjacent seaward slopes of the Dividing Range, its occurrence in places extending inland for a distance of up to

160 km (F.T.B., 1953, 1957). Its latitudinal range is from 24^0 to 36^0S (Eldridge *et al.*, 1994), while altitudinally it occurs from just above sea level to 300 m in the South and to almost 1200 m in the north (Poynton, 1979).

The climate is warmer temperate to subtropical and humid. Mean maximum and mean minimum temperatures for the warmest and coolest months respectively range from 28^0 to 30^0C and from about 3 to 4^0C (Jacobs, 1976). Rainfall averages from 900 to 1200 mm a year and occurs mainly during summer in the north but is fairly uniformly distributed in the south (F.T.B., 1953).

E. saligna grows to a height of 40 to 45 m and a diameter of 120-180 cm producing a well-formed straight bole which reaches to between half and two-thirds of its overall height (F.T.B. 1953; Jacobs, 1976).

2.4.2. *E. tereticornis*

E. tereticornis Smith has several synonyms as follows :

E. umbellata Gaerkum Damin (Blakeley, 1965)

E. semisupera R.Br. ex Maiden (Odermatt, 1985)

E. tereticornis is very widely distributed on the seaward side of the Dividing Range in eastern continental Australia. It grows in a long narrow strip from southern Papua New Guinea to Victoria, Australia, a range exceeding 30^0 of latitude, within 100 km of the sea (Eldridge *et al.*, 1994). Altitudinal adaptation of the species is very wide. It naturally grows just from above sea level to 900 m in Australia (Odermatt, 1985), specifically to 350 m in Victoria, to 750 m in New South Wales and to 900 m in Queensland; it grows to 1850 m in Papua (Poynton, 1976).

The climate varies within wide limits, from markedly wet and dry monsoonal seasons at 9^0S in Papua New Guinea to a dominating summer rainfall with a very dry winter in Queensland, an

equal winter/summer rain distribution in southern New South Wales and a dry summer and cold wet winter at 38^0S in eastern Victoria (Eldridge *et al.*, 1994). It grows on an altitude range of from sea level to 1000 m with an annual rainfall of 500-1500 mm.

E. tereticornis is a moderately large tree that grows up to a height of 40-46 m or more and a diameter of 90-190 cm (F.T.B, 1957). It usually has a straight trunk, reaching to at least half its height and it forms a large, somewhat open crown (Poynton, 1979).

2.4.3. *E. urophylla*

Syn.: *E. alba* Auct., non Reinwardt ex Blume

E. alba decaisneana Ined.

E. decaisneana Auct; non-Blume; *E. decaisneana*

E. urophylla is endemic in the Sunda Islands, more specifically in the triangle formed by Timor in the south, Flores in the northwest and Wetar in the north east (Martin and Cossalter, 1975-1976). Within this triangle are the islands of Adonara, Alor, Lomblen and Pantar in which scattered stands of *E. urophylla* were found (Eldridge *et al.*, 1994). The isolation of the Islands by the Flores and Timor seas restrict the species` latitudinal distribution from 7.5^0 to 10^0S and longitudinally, being less precise, is set between 122^0 to 127^0E (Eldridge *et al.*, 1994; Martin and Cossalter, 1975; Jacobs, 1976; Blakes; 1977). Altitudinal range of the species ranges from 1000-2960 m above sea level in Timor, 300-1100 m in Flores, Adonara, Lomblen, Pantar and Alor and from 70 m to above 800 m in Wetar (Eldridge *et al.*, 1994).

The natural distribution is within dry and wet climatic zones with two to eight dry months a year and mean annual rainfall ranging from 600 to 2500 mm. Temperatures vary remarkably with altitude. Mean maximum temperatures vary from 27^0-30^0 C at 400 m to only 17^0-21^0 C at 1900 m

(Eldridge *et al.*, 1994). In Timor, rainfall is abundant (1300-2200 mm) with three to four dry months and mist and fog are common (Eldridge *et al.*, 1994). It occurs on mountain slopes and in valleys. Best development occurs in Timor on moist, deep, well-drained soils generally derived from volcanic and metamorphic rocks. It commonly grows on basalts, schists and slates but is rarely found on limestone soils.

E. urophylla is a forest tree of exceedingly variable stature and habit. It usually grows to a height of 25-45 m and 1 m in diameter producing a clean, slender bole for half to two thirds of its height (Eldridge *et al.*, 1994) that in course of time may become buttressed at the base (Martin and Cossalter, 1975-1976). At an altitude of 2900 m it assumes a shrub form no more than 3.5 m tall. Exceptional individuals can reach 55 m in height and 2 m in diameter. It is one of the best low altitude eucalypt species for planting in the tropics (Eldridge *et al.*, 1994).

2.4.4. *Grevillea robusta*

The natural distribution of *G. robusta* A cunn. Ex R.B. (Silky oak) has been reported by a number of authors namely Swain (1928); Lebler (1979); Harwood (1989); Harwood (1992) and Makinson and Boland (1992). It grows naturally in northern New South Wales and Southern Queensland from the coast to a maximum of 160 km inland (Harwood, 1992). The altitude ranges from sea level to a maximum of 1120 m in Queensland (Harwood and Getahun, 1989). The latitudinal range extends over some 470 km from 30.5^0 10'S in the Guy Fawkes and Orara river catchments in New South Wales to 25^0 50' north of Gympie, Queensland, a distance of 500 km (Harwood, 1989).

G. robusta is found in two distinct habitat types (Harwood 1989,1992), The first is along the banks of rivers and streams, usually within a short distance of water's edge. The second habitat group for the species contains the vine forest and thickets dominated by *Araucaria cunninghamii* which often cover large areas, including steep upper valley slopes and rolling terrain well away from rivers.

Climate varies widely within the natural range despite the small geographic area involved, probably due to substantial altitudinal range and the rainfall gradient created by prevailing weather systems interacting with rugged topography (Harwood, 1992). Mean annual temperatures range from 14.7 to 20^{0}C and annual rainfall from 720 to 1719 mm. The sites with lowest precipitation are generally furthest inland, although, topography influences rainfall distribution so that high altitude sites tend to be wetter (Harwood, 1992). *Grevillea robusta* grows on fertile, well-watered environments (Harwood, 1989). It prefers deep, soft red basaltic or black alluvial loams (Swain, 1928).

2.4.5. *Pinus caribaea*

P. caribaea Morelet (Caribbean pine) includes three varieties namely: *P. caribaea* var. *bahamensis* (Grisebach) Barret et Golfari (syn. *P. bahamensis* Grisebach); *P. caribaea* var. *hondurensis* (serie clause) Barret et Golfari (syn. *P. hondurensis* sénéclauze, *P. hondurensis* Loock) and *P. caribaea* var. *caribaea*.

P. caribaea has a wide but very disjunct distribution in the Caribbean basin and varies much, both morphologically and silvilculturally (Poynton, 1977). *P. caribaea* var. *caribaea* is confined to Cuba and the Isle of the pines, *P. caribaea* var. *bahamensis* to certain islands of the Bahamas and Caicos group and *P. caribaea* var. *hondurensis* to Central America. In Cuba, *P. caribaea* var. *caribaea* occupies low rolling hills and mountain slopes in the west, ascending to 330 m. It forms open forest of limited extent and sometimes associated with *P. tropicalis* or with sundry hardwoods (Luckoff, 1964). *P. caribaea* var. *bahamensis* (endemic in the Bahamas) is restricted to the four northeasterly Islands of the group namely: Grand Bahamas, Great Abaco, Andros and New Providence.

In Caicos group, the occurrence of the species is limited to the Islands of North Caicos and Pine Cay, which marks the most easterly extension of the species range. In Central America, *P. caribaea* var. *hondurensis* is found in British Honduras, Guatemala, the Republic of Honduras,

(including the Islands of Guanaja or Bonaca) and in Nicaragua (Farjon and Styles, 1997). It is mainly distributed on the lowland coastal plains within the Atlantic climatic influence, from the edge of the mangrove swamps to lower upland bunch-grass/pine savannas. In Nicaragua it is the southern most pine in the Americas (Farjon and Styles, 1997).

The overall distribution of *P. caribaea* inclusive of its varieties reaches latitudinally from 12^0 to 27^0N and longitudinally from 12^0 to 90^0W (Critchfield and Little, 1966). Lamb (1973) gives the natural distribution of the species to be between latitudes 23^0 13'N near the east of Nicaragua to 27^0 25'N in Grand Bahamas and Great Abaco and longitudinally from 71^0 25'W on Carico Islands to 89^0 25'W at Poptun in Peten Province, Guatemala.

For the most part, trees occur at relatively low elevations, but in Central America, it is not infrequently encountered at an altitude of approximately 760 m where in rare instances it ascends to 1200 m (Poynton, 1977). The climate is tropical to subtropical and humid, with summer rainfall averaging from 1000 to 1500 mm/year (Luckoff, 1964). Frost and snow are unknown and weather conditions at the coast are equable, and even inland the temperature rarely, if ever, falls below 9^0C or rises above 37^0C (Poynton 1977).

The species occurs on a wide variety of sites and soils. In the Bahamas and Caicos Islands, where the soils are almost non-existent, the trees are rooted on a porous limestone formation with a very high water table, which fluctuates with tides (Luckoff, 1964). In Cuba, the species is found on shallow, well drained loam soils, overlying shales and sandstones and on deep, lateritic soils derived from serpentine (Poynton, 1977).

On the Isle of Pines and on the coastal plains of British Honduras, where soil characteristics largely determine its distribution, the tree is practically confined to leached, shallow sand overlying clay (Poynton, 1977). The site is subject to water logging during the rainy season but becomes very dry in time of drought.

In the interior of British Honduras, Guatemala and the Republic of Honduras, the soils, though leached, are of somewhat better quality, consisting of clays, sands-clays or loams derived from granites, porphyries and tuffs (Poynton, 1977).

The tree is of moderately large size, seldom exceeding a height of 18-30 m and a diameter of 25-75 cm. Lamb (1973) reports a maximum height for the species to be 45 m and 135 cm diameter when grown under best conditions on the Mountain Pine Ridge in British Honduras.

2.4.6. *P. kesiya*

P. kesiya Royle ex Gordon Syn.: *P. insuralis* Endlicher, *P. khasya* Royle (Poynton, 1977) and *P. langbianensis* and *P. yunnanensis (*Styles and Burley, 1972). It is a very variable species, having a wide but scattered distribution in southeastern Asia and the Philippine Islands. In the Philippines the principal occurrence is in the Central Cordillera of Northern Luzon, where it is found at altitudes between 750-2300 m above sea level (Cooling, 1967; Mirov, 1967).

In the Asian mainland, its range extends from Vietnam westwards through Laos, Cambodia, Thailand, the Yunnan Province of China and Burma to the Khasi Hills in Assum (Poynton, 1977). Its latitudinal range lies between 11 and 29^{0}N, while its longitudinal range is from 26 to 119^{0}E (Critchfield and Little, 1966). It grows from 900 to 1800 m above sea level in the east and from 750 to 2400 m in the west. The species grows on warmer temperature to subtropical and humid to sub humid sites (Troup, 1921). Temperatures vary between extremes of -1 to 28^{0}C. Rainfall is monsoonal, ranging from 1780 to 4450 mm per year. The tree is exposed to a dry season from 4 to 6 months in winter. It is found on soils of many different types derived from such diverse parent materials as basalt andesite, granite, schist and sandstone (Poynton, 1977). While often clayey in consistency, the soils are invariably well drained and the species does not tolerate swampy conditions. It is a moderately large, fast growing tree. On favourable sites in the Philippines, *P. kesiya* attains a height of 30-46 m and a diameter of 60 to 150 cm (Cooling, 1967; Dallimore and Jackson, 1966).

2.4.7. *P. patula*

P. patula Scheide ex Schlechtendal & Chamisso and its variety *longepedunculata* have a restricted and disjunct distribution in the temperate humid regions of south-central Mexico, where the former is more or less confined to the southern Sierra Mandrel Oriental and the latter to the Sierra Madre Del Sur (Poynton, 1977). The species in its typical form occurs in the States of Hidalgo, Puebla and Vera Cruz, and also found sporadically in Nuevo Leon, Tamaulipas, Queretaro, Mexico and Mexico city crossing the border thence in northern Oaxaca (Robertson, 1932-34, Loock, 1950; Mirov, 1967; Barrett, 1972).

Latitudinal distribution of the proper species lies between 18^0 and 24^0N, and that of the variety between 17^0 and 18.5^0N (Poynton, 1977). At the northern limit of its range, the species occurs at an altitude of 2300 to 2500 m above sea level, but in the south it ascends to 2700 m. The variety *longepedunculata* is found at elevations of up to 3000 m.

The climate varies from temperate to cooler temperate and humid. Mean annual temperature varies between 10^0 and 19^0C. Frost in higher elevations is fairly severe (Poynton 1977). Rainfall averages from 1000 to1350 mm/year, most of it taking place during summer months, when the humidity is high (Poynton 1977). The species reaches its best developments in ravines and on flats where the soil is deep, moist, well drained and of a loamy or sandy consistency (Loock, 1950).

A medium-sized to large tree, *P. patula* grows to a height of 30 m or more and a diameter of 100 cm, producing a fairly straight, clean bole up to 15 m. Trees developing in dense stands are fairly light branched, although open grown individuals develop robust, horizontal or slightly drooping branches (Poynton, 1977).

2.4.8. *P. maximinoi*

P. maximinoi H.E. Moore occurs naturally in Mexico, mainly in the southern half, in Sinaloa, Jalisco, Michoacan, Mexico, Hidalgo, Tlaxcala, Puebla, Vera Cruz, Guerrero, Oaxaca and Chiapa and in the mountainous parts of Guatemala, Honduras, El Salvador, and north-west Nicaragua (Styles and Faljon, 1997). The species has wide ecological amplitude, occurring from wet subtropical forest, where it is a gap pioneer, to cooler cloud forests on high mountains of Mesoamerica. It has a great altitudinal range, extending from 450-2800 m, with an optimum at 900-1800 m. It occurs on a variety of soils under various climatic conditions. In Mesoamerica, precipitation is 900-2500 mm per annum. *P. maximinoi* is a tree of medium to tall height, attaining a height of 20-40 m and a diameter of 70-90 cm. The trunk is monopodial, straight, with lower half of the bole free from branches (Faljon and Styles, 1997).

2.4.9. *P. tecunumanii*

P. tecunumanii is distributed from low to high montane regions of Chiapas (Mexico), Guatemala, Belize, Honduras, El Salvador and Nicaragua. The altitudinal range is wide, ranging from 300-2900 m (Faljon and Styles, 1997). It naturally grows in areas that receive at least 1000 mm annual rainfall and up to 2500-3000 mm in some places. It experiences a long dry season (seven months) and fire at lower to middle altitudes is an integral part of its ecosystem (Faljon and Styles, 1997). The species grows in open to closed canopy pine and pine-oak forests, with tall trees, attaining a height of 50-55 m and a diameter of 140 cm. It produces straight boles usually clear of branches for 20-30 m above the ground (Faljon and Styles, 1997).

3. MATERIALS AND METHODS

This chapter gives the following: description of study sites; seed sources and details; experimental designs; field procedures; assessment procedure for investigated traits and statistical analyses methods used.

3.1. Description of the trials

3.1.1. Climate and soils of experimental sites

The description of trial sites is summarized in Table 3.1.

3.1.2. Seed sources

3.1.2.1. *Eucalyptus saligna*

The trial includes five seed sources of *E. saligna*, one from each of the following countries: Australia, Kenya, Malawi, Tanzania, and Rwanda (Table 3.2). Apart from the Australian provenance, other sources originated from secondary introductions of unknown origins.

3.1.2.2. *E. tereticornis*

This experiment is a combined progeny and provenance trial, with 17 seed lots from five sources (Table 3.3). Three of the five sources are from Australia, one from Malawi and one from Rwanda.

Table 3.1: Location, altitude, climate, slope, aspect and soils of sites for nine species in ten seed source trials in Rwanda.

Species	Site	Lat (S)	Long (E)	Alt (m)	MAP* (mm)	MAT+ (C)	Slope (%)	Aspect	Soil type	Comments
Eucalyptus saligna	Ruhande Arboretum	2° 33'	29° 30'	1700	1232	19	16	Northerly	Humic ferralitic[1]	Daily temperature maxima range from 28.5°C (April) to 32°C (September) and corresponding minima from 10°C (April) to 9° C (September). Soils are shallow.
E. tereticornis	Ruhande Arboretum	2° 33'	29° 46'	1700	1231	19	15.5	Southerly	Humic ferralitic[1]	Same as for *E. saligna*
E. urophylla	Ruhande Arboretum	2° 33'	29° 46'	1700	1231	19	16	Northerly	Humic ferralitic[1]	Same as for *E. saligna*
Grevillea robusta	Ruhande Arboretum	2° 33'	29° 46'	1700	1232	19	20	Easterly	Humic ferralitic[1]	Same as for *E. saligna*
Pinus caribaea	Kiyombe, Byumba	1° 25'	30° 05'	1900	1900	16	25	Northerly	Kaolisols[2]	Shallow and stony site
P. kesiya	Rusumo, Kibungo	2°20'	30° 30'	1550	1000	-	50	Northerly	Lateritic[2]	Shallow and stony site
P. maximinoi	Musebeya, Gikongoro	2° 55'	29° 50'	1900	1200	19	15	Easterly	Unclassified[3]	Site is on a high potential area with deep, fertile soil
P. patula[1]	Nyamugali, Ruhengeri	1° 40'	29° 50'	2325	1207	16	60	Southerly	Unclassified[2]	Site is on a high potential area with deep, fertile soil
P. patula[2]	Mushubati Gitarama	2° 10'	29° 45'	1900	1200	19	15	Northerly	Unclassified[2]	Shallow and stony site
P. tecunumanii	Musebeya, Gikongoro	2° 55'	29° 25'	2400	1500	-	7.5	Easterly	Hygrokaolisols[3]	Site is on a high potential area with deep, fertile soil

***Mean annual precipitation is bimodal on all sites (February-May, October-December). [1]Egli and Pietrowicz (1990); Gasana (1973), Reynders (1961).**

[2]Information obtained from Ruhande Arboretum (CGF) data bank. [3]Kalinganire (1996). +Mean annual temperature [1]*P. patula on* site I. [2]*P. patula on* site II.

3.1.2.3. *E. urophylla*

The trial is comprised of four seed sources, two from the species range in Indonesia, another from Rwanda and one from unknown origin, imported from SETROPA, a Netherlands seed company (Table 3.4).

Table 3.2: Seed source and particulars of *E. saligna* provenance trial in Ruhande Arboretum (Butare) Rwanda.

Serial No.	Code	Source	Country	Lat (S)	Long (E)	Alt (m)	Date collected
1	83/3979N	Kangaroo River	Australia	29^0 43'S	152^0 7'E	21	-
2	Batch No. 1473	Lushoto	Tanzania	4^0 47' S	38^0 7'E	1510	1984
3*	Batch No. 492-072	Masaita	Kenya	0^0 05'S	36^0 00'E	-	1983
4*	1589	Zomba Plateau	Malawi	15^0 12'S	35^0 34'E	-	1984
5*	-	Kibuye	Rwanda	2^0 31'S	29^0 44'E	1900	1982

***Locational variables estimated from a map**

Table 3.3: Seed source and particulars of *E. tereticornis* provenance trial in Ruhande Arboretum.

Serial No.	Code	Source	Country	Latitude (S)	Longitude (E)	Altitude (m)
1	1878	Spearhead farm	Malawi	-	-	-
2	10706	Mt. Garnet, QLD	Australia	18^0 30'	144^0 45'	875
3	10693	Mt. Garnet, QLD	Australia	18^0 30'	144^0 45'	875
4	10691	Mt. Garnet, QLD	Australia	18^0 30'	144^0 45'	875
5	10701	Mt. Garnet, QLD	Australia	18^0 30'	144^0 45'	875
6	10696	Mt. Garnet, QLD	Australia	18^0 30'	144^0 45'	875
7	10660	Halenvale, QLD	Australia	15^{0}45'	145^0 45'	100
8	10656	Halenvale, QLD	Australia	15^{0}45'	145^0 45'	100
9	10655	Halenvale, QLD	Australia	15^{0}45'	145^0 45'	100
10	10651	Halenvale, QLD	Australia	15^{0}45'	145^0 45'	100
11	10649	Halenvale, QLD	Australia	15^{0}45'	145^0 45'	100
12	10618	Laura River, QLD	Australia	15^0 45'	145^0 14'	100
13	10615	Laura River, QLD	Australia	15^0 45'	145^0 14'	100
14	10619	Laura River, QLD	Australia	15^0 45'	145^0 14'	100
15	10621	Laura River, QLD	Australia	15^0 45'	145^0 14'	100
16	10616	Laura River, QLD	Australia	15^0 45'	145^0 14'	100
17*	-	Butare	Rwanda	2^0 36'S	29^0 47'E	1700

***Locational variables estimated from a map.**

Table 3.4: Seed source and particulars of *E. urophylla* provenance trial in Ruhande Arboretum, Butare Province, Rwanda.

Serial No.	Code	Source	Country	Latitude	Longitude	Altitude (m)	Date collected
1	8028098 N	West Alor	Australia	8^{0}20'S	124^{0}27'E	500	1979
2*	SN: 11786	Flores Islands	Indonesia	8^{0}36'S	122^0 42'E	-	-
3	-	Unknown	-	-	-	-	-
4	-	Ruhande Arboretum	Rwanda	2^{0}33'S	29^{0}30'E	1700	-

*** Locational variables for seed source No. 2 were estimated from a map.**

3.1.2.4. *Grevillea robusta*

The trial includes seven provenances from Australia of which five were from natural forests and two from plantations of unknown origin, and one local source (Table 3.5). The local seed source originated from secondary introductions (imported from Kenya) of unknown origin (Harwood *et al*, 1992).

Table 3.5: Seed sources and particulars of *G. robusta* provenances in the trial in Ruhande Arboretum, Butare (Rwanda).

Serial No.	Parent Stand	Date Collected	Source	No. of parents	Lat (S)	Long (E)	Alt (m)	MAP* (mm)	MAT** (°C)
41	Natural	5.1.87	Imbil, Australia	10	26°80'	152°40'	100	1200	20.0
42	Plantation	16.1.87	Pechey, Australia	10-20	27°17'	152°04'	600	900	17.1
44	Plantation	30.12.85	S.F.28 Coominglan, Austr	4	24°47'	150°49'	500	780	18.1
46	Natural	24.12.86	Glastonbury Recn. Area, S.F.82 Brooyar, Australia	3	26°10'	152°30'	100	950	20.4
48	Natural	14.1.86	S.F.Gallangowan, Australia	6	26°23'	152°20'	400	850	18.2
49	Natural	30.1.87	Muddy Logging Area, Benarkin, Australia	10	26°47'	152°11'	280	990	18.9
50	Plantation	10.7.86	Shyanda, Butare, Rwanda	>20	2°33 '	29°46'	1700	1200	19.1
52	Natural	23.12.86	S.F. 50 Parish of Glenbar, Australia	5	25°50'	152°20'	200	1042	19.9

***Mean annual precipitation. **Mean annual temperature**

3.1.2.5. *Pinus caribaea*

The trial is comprised of 13 provenances. Seven of the sources were obtained from Honduras, three from Guatemala, and one from Australia, one from Mount Pine Ridge, Belize and one from Kenya (Table 3.6). All seed for the experiment was imported from DANIDA. No location details regarding the latitudes and longitudes of seed origin were provided.

Table 3.6: Seed source and details of *P. caribaea* provenances in Kimandwa, Kiyombe District, Byumba Province.

Serial No.	Code	Source	Country	Altitude (m)
1	1141/83	Pinaleja, St. Barbara	Honduras	300-650
2	1139/83	Dulce, Nombre Culmi	Honduras	400-600
3	1133/83	Languin, Alta Verapaz	Guatemala	-
4	1165/83	Cardwell, Queensland	Australia	20
5	1137/83	Limones, El Paraiso	Honduras	600-800
6	1134/83	Poptun Peten	Guatemala	-
7	-	-	Kenya	-
8	1155/83	Mt. Pine Ridge	Belize	-
9	1060	Mosquitia, Gracia a Dios	Honduras	30-140
10	5514	Yojoa Lake, St. Barbara	Honduras	600-700
11	1143/83	Guanaja	Honduras	0-300
12	5518	San Carkos - Yoro	Honduras	350-450
13	-	Poptun Peten (Commercial lot)	Guatemala	-

3.1.2.6. *P. kesiya*

The trial consists of 12 seed sources five of which were from Thailand, two from Colombia, two from Zimbabwe, one from Malawi, one from the Philippines and one local seed source (Table 3.7). The local one originated from South Africa.

Table 3.7: Seed source and details of *P. kesiya* provenances in Rusumo District, Kibungo Province.

Serial no.	Code	Source	Country	Latitude	Longitude	Altitude (m)	Rainfall (mm)	Collection date
1	SETROPA*	Penhalonga-Mukandi	Zimbabwe	18^0 43' S	32^0 51' E	1268	1725	1984
2	DANIDA no. 1104/83	Chieng-Moi Muwang-Doi Suthep	Thailand	18^0 46' N	99^0 00' E	1100-1800	-	1984
3	DAN. No. 1233/83	Rizal Filipinos	Colombia	121^0 10' N	15^0 45'W	1500	-	-
4	DAN. No. 1095/83	Chiengmoi-Hod-Mae	Thailand	18^0 10' N	98^0 15' E	1200	-	1979
5	DAN. No. 1096/83	Maesoir-Chiengmoi	Thailand	19^0 00' N	98^0 45' E	1050	-	1979
6	DAN. No. 1097/83	Chiengmoi-Om Koi-Nong Krating	Thailand	17^0 56' N	98^0 17' E	1080	-	1974
7	DAN. No. 1101/83	Chiengmoi- Om Koi Pang Ong Mong	Thailand	17^0 56' N	98^0 17' E	1000	-	1977
8	DAN. No. 1234/83	Rizal Filipinos Luzon	Colombia	121^0 10' N	15^0 45'W	1500	-	-
9	SN 1710/83	-	Malawi	-		-	-	1981
10	TZ Batch no. 238	-	Philippines	-	-	-	-	-
11	-	Ruhande Arboretum	Rwanda	20^0 33' S	29^0 36' E	1706	1200	1984
12	SN 12389	Rupere, Mugunyana	Zimbabwe	18^0 44' S	32^0 49' E	1050	1756	1982

***Netherland`s commercial seed supplying company**

3.1.2.7. *P. patula*

The species has been raised in two different trials each comprised of different seed sources, but five from the species range being common to both trials. Site I is located in Muhanga-Ndiza, Mushubati District, Gitarama Province and site II is in Rwerere, Nyamugali District, Ruhengeri Province. The trial on site I is made of 28 provenances from different sources (Table 3.8a) and site II comprises of 12 seed sources, all from Mexico (Table 3.8b).

3.1.2.8. *P. maximinoi*

The trial comprised of five seed sources. All seed lots were imported from Guatemala. Only one seed source has an elevation lower than the experimental site in Rwanda (Table 3.9).

Table 3.8(a): Seed source and particulars of *P. patula* seed sources trial for site I.

Serial No.	Code	Source	Country	Latitude	Longitude	Altitude (m)	Date collected
1*	-	Tamira	Rwanda	2^0 30'S	29^0 28'E	1750	1985
2*	034103	Kinale	Kenya	0^0 39'S	36^0 39'E	-	1982
3*	DAN. 5208	Zomba Plateau	Malawi	15^0 18"s	35^0 18'E	1750	-
4	L67	Acaxatitlen	Mexico	20^0 90' N	98^0 10' W	2030	1980
5	L214	Huachinango	Mexico	20 10' N	98 10' W	2030	1968
6	L464	La Venta	Mexico	19 20' N	99 30' W	2300	1975
7	L769	Tlaixtlipa	Mexico	20 03' N	98 04' W	2000	1979
8	L770	Rancho Thacotha	Mexico	19 41' N	98 08' W	2760	1979
9	L383	Pinale de Amdes	Mexico	20 40' N	98 41' W	2050	1978
10	L764	Pinale de Amdes	Mexico	20 08' N	98 42' W	2350	1980
11	L771	Altotnga	Mexico	19 45' N	97 15' W	2210	1979
12	Commercial lot	Stapleford	Zimbabwe	18 44' S	32 40' E	1760	1984
13	Commercial lot	Chimanimani	Zimbabwe	19 53' S	32 48' E	1504	1984
14*	034107	Kibata I	Kenya	0^0 12'S	36^0 42'E-	-	1983
15	1146/83	Berlin	RSA	25 33' S	34 44' E	1341	-
16	1147/83	Ceylon	RSA	25 05' S	30 46' E	1372	-
17	1106/83	StapleFord	Zimbabwe	18 44' S	30 49' E	1760	-
18	1148/83	Belfast	RSA	15 44' S	30 01' E	1888	-
19*	1116/83	Kinale	Kenya	0^0 39'S	46^0 39'E	-	-
20	1145/83	Tweefontein	RSA	20 03' S	30 47' E	1152	-
21*	1115/83	Kiamweri	Kenya	$00^0$23' S	37^0 56'E		-
22	12388	Rupere	Zimbabwe	18 44' S	32 49' E	1050	1983
23	5200	Zomba Plateau	Malawi	15^0 12"s	35^0 34'E	1750	-
24	1149/83	Frankfurt, Transvaal	RSA	25 02' S	30 53' E	1050	-
25	1151/83	Wilgeboom	RSA	24 56' S	30 57'E	945	-
26	1150/83	Bergvliet	RSA	25 04' S	30 53' E	983	-
27	1152/83	DR. de Wet FRS	RSA	25 02' S	30 53' E	1005	-
28*	-	Gisovu	Rwanda	2^0 32'S	29^0 17'E	2300	1985

Locational variables estimated from a map

Table 3.8(b): Particulars of seed sources of *P. patula* from Mexico included in the trial for site II.

Serial No	Code	Source	Latitude (N)	Longitude (W)	Altitude (m)
1	769	Tlaixtlipa	20^0 03'	98^0 04'	2000
2	214	158-159-km Huachinango	$20^0$10'	98^0 10'	2030
3	770	37-km-Apizaco Chignahuapan	$19^0$41'	98^0 08'	2760
4	764	Pinal de Amdes	$20^0$08'	99^0 42'	2350
5	764	5-km-Acaxotitlan Tejocotal	$20^0$09'	98^0 10'	2030
6	645	La-Joya-Rancho Palelquillo	$19^0$36'	97^0 08'	2250
7	510	La Venta D.F	$19^0$20'	99^0 30'	2500
8	768	La Joya	$19^0$36'	97^0 08'	2160
9	641	Zacualtipan Tianguistenango	$20^0$40'	98^0 40'	2000
10	771	Altotonga	$19^0$45'	97^0 15'	2210
11	644	La Joya	$19^0$36'	97^0 08'	2100
12	402	Zacualtipan Tianguistenango	20^0 40'	98^0 40'	2000

3.1.2.9. *P. tecunumanii*

The trial comprised five seed sources, three from Guatemala and two from Nicaragua (Table 3.10).

Table 3.9: Particulars of seed sources of *P. maximinoi* provenances from Guatemala included in the trial in Musebeya District, Gikongoro Province.

Serial no	Code	Source	Country	Latitude (N)	Longitude (W)	Altitude (m)	Collection date
1	1312/84	Santa Rosita	Guatemala	14° 38'	90° 29'	1600	1984
2	1314/84	Chitul-Alta-Verapaz	Guatemala	15° 24'	90° 23'	1500	1984
3	1313/84	Santa Jeronima Baja Verapaz	Guatemala	15° 01'	90° 18'	1500	1984
4	1315/84	San Raimundo	Guatemala	14° 44'	90° 37'	1600	1984
5	1311/84	Petensito-San-Cristobal Alta Verapaz	Guatemala	15° 21'	90° 28'	1350	1984

Table 3.10: Seed source and details of provenances of *P. tecunumanii* in Musebeya District, Gikongoro Province.

Serial no	Code	Source	Country	Latitude (N)	Longitude (W)	Altitude (m)
1	1257/84	La Soledad	Guatemala	14° 31'	90° 09'	2300-2600
2	1260/84	San Lorenzo	Guatemala	15° 07'	89° 41'	2000-2200
3	1324/84	San-Raphael-del- Norte	Nicaragua	13° 14'	86° 08'	1200
4	1325/84	Yucul	Nicaragua	12° 55'	85° 49'	900
5	1259/84	Basque San Jeronima	Guatemala	15° 01'	90° 18'	1800

3.1.3. Experimental design and field procedures

All trials were laid out in a randomised complete block design with varying numbers of replications (Table 3.11). Planned thinnings were highly affected by war and genocide in the country and only a few (or no) thinnings were done. Where done, 30% of the initial stocking was removed during the first thinning. Site preparation and maintenance of the experiment were done manually for all trials.

Table 3.11:Experimental designs and field procedures for nine species in ten trials of common or promising plantation tree species in Rwanda.

Experimental design					Field procedures	
Species	**Reps.**	**Plot size***	**Spacing (m)**	**Comments**	**Date establ.**	**Description**
Eucalyptus saligna	3	1 x 21	2.5 x 2.5		23.11.1986	Thinning done in 1992
E. tereticornis	4	1 x 12	2 x 2	Progeny and provenance test	17.11.1986	Thinning done in 1992
E. urophylla	4	1 x 20	2.5 x 2.5		2.10.1986	Thinning done in 1992
Grevillea robusta	4	1 x 10	2.5 x 2.5		4.3.1988	Thinning done in 1997
Pinus caribaea	9	1 x 10	3 x 3		26.10.1988	No thinning at all
P. kesiya	7	1 x 15	3 x 3		20.2.1985	Thinning done in 1997
P. patula I	5	1 x 10	3 x 3		-.10.1985	No thinning at all
P. patula II	3	6 x 6	2 x 2		-.12.1986	No thinning at all
P. maximinoi	5	1 x 10	2.5 x 2.5		1987	No thinning at all
P. tecunumanii	5	1 x 10	2.5 x 2.5		1987	No thinning at all

*All plots except the one for *P. patula* (site II) are linear

3.2. Field assessment

3.2.1. Previous assessment

Apart from the final assessment, all trials were assessed at least once previously. The frequency of the assessment depended on resources availability and this was seriously affected by war and genocide in the country during the period 1990-1994 and beyond. Common traits assessed in all trials included survival, diameter at breast height and total tree height. Stem straightness was also measured in some trials. Previous data for all trials were obtained from the ''Centrale des Graines Forestieres'' database. Dates of assessment for different trials are presented in Table 3.12.

Table 3.12: Frequency and year of assessment of ten seed source trials of exotic plantation tree species in Rwanda.

Species	**Year**							
	Establi-Shed	**Assessed***						
Eucalyptus saligna	1986	1987(1)	1989(2)	1996(10)	2001(15)	-	-	-
E. tereticornis	1986	1987(1)	1988(2)	1989(3)	1992(6)	1995(9)	1997(11)	2001(15)
E urophylla	1986	1987(1)	1989(3)	1992(6)	1996(9)	2001(15)	-	-
Grevillea robusta	1988	1989(1)	1990(2)	1993(5)	1997(8)	2001(13)	-	-
Pinus caribaea	1988	1989(1)	2001(13)	-	-	-	-	-
P. kesiya	1985	1986(1)	1988(3)	1999(14)	2001(16)	-	-	-
P. maximinoi	1987	1990(3)	2001(14)	-	-	-	-	-
P. patula[1]	1985	1986(1)	1989(4)	2001(16)	-	-	-	-
P. patula[2]	1986	1987(1)	2001(15)	-	-	-	-	-
P. tecunumanii	1987	1991(4)	2001(14)	-	-	-	-	-

[1]***P. patula*** **on site I;** [2]***P. patula*** **on site II.** *Figures in parentheses indicate age in years at assessment.

3.2.2. Final assessment

The final assessment was done in May-July, 2000. Details of the traits measured and the methodology used are described below.

3.2.2.1. Survival rate

The number of surviving trees per plot was recorded and expressed as a percentage of the initial number of trees in the plot.

3.2.2.2. Diameter at breast height (DBH)

For each plot, all surviving trees or net plots were measured for DBH using a caliper. DBH values were taken at 1.3 m above ground and recorded to the nearest 0.1 cm.

3.2.2.3. Total tree height

All surviving trees in each plot were measured for total tree height using a Haga altimeter. Height values were recorded to the nearest 0.1 m.

3.2.2.4. Stem straightness

For stem straightness assessment, all trees in a plot were considered. Subjective means were used in assigning scores to an individual tree. A 1-8 scale was used in the final assessment occasion, where 1 represented very crooked and buttressed trees and 8 represented straight and almost cylindrical trees with good form. In previous assessments, this trait was also assessed subjectively in some trials using a scale of 1-3 in which case 1 was assigned to very crooked trees and 3 to very straight ones.

3.2.2.5. Branching pattern

This trait was only assessed during the final assessment occasion. A similar scale as for stem straightness was employed where 1 represented individuals with dense, very large and vertical (close to 0^0) branches and 8 represented trees with sparse, small and horizontal (close to 90^0) branches.

3.3. Data analyses

Statistical analyses were carried out using SAS-PC (SAS Inst. Inc.,1982). For each experiment and each plot, survival percentage, DBH (cm), height (m), stem straightness, branching pattern and mean tree volume (m^3) attributes were subjected to analysis of variance of plot means. Survival percentage data were subjected to arcsine transformation prior to analysis of variance (ANOVA) (Ott, 1993) and significantly different means were separated using Least Significant Difference (LSD) and Student Newman Keuls (SNK) methods for small and large trials respectively. Stem form values previously assessed at the 1-3 scale were converted to the 1-8 scale by multiplying plot mean scores by 8/3. The model used for ANOVA was of the form:

$$Y_{ij} = \mu + B_i + P_j + e_{ij}$$

where Y_{ij} is the plot mean performance of the *j*th provenance in the *i*th block, μ is the overall mean, B_i is the effect of the *i*th block, P_j is the effect of the *j*th provenance, and e_{ij} is the random error of the *ij*th plot mean. Seed sources were considered as fixed effects. Correlation analyses were also done to investigate juvenile-mature relationships and trait-trait correlation in survival and growth parameters based on final assessment plot means. The age-age and trait-trait correlation referred to in this study is phenotypic. Its usefulness in predicting growth and yield as well as in selecting for best seed lots is based on the assumption that phenotypic correlation is directly related to genetic and not only a result of the effect of the environment. Correlation between the performance of seed sources and the characteristics of the sites of origin was also

investigated on selected trials, namely *Grevillea robusta, Pinus kesiya* and *P. patula.* In this case, provenance means in terms of diameter and height growth were correlated with locational variables (latitude and altitude) of seed origin. The idea of 'adjusted latitudes' was also attempted. This was first suggested by Wiersma (1963) that in a growing season (number of days with a mean daily temperature >6 ^{0}C) an increase of 1^0 latitude corresponds to an increase of 100 m in altitude. In this study however, the number of days in a growing season was considered uniform in the study sites. The adjusted latitudes were therefore taken as follows:

ADLAT = (AL + ALT/100)

where:

ADLAT = adjusted latitude;

AL = Actual latitude (decimals), and

ALT = altitude (m).

Mean total tree volume (under bark) per plot was estimated using Schumacher and Hall volume model (Bredenkamp, 2000) (equation 1 below). The same model is used to estimate under bark tree volume and different coefficients for specific tree species have been developed. Species in this study whose coefficients are known include *P. caribaea* and *P. patula.* Volume for *E. saligna* was calculated using coefficients for *E. grandis* (Bredenkamp, 2000) as the two species were assumed to have similar forms.

$LnV=b_o+b_1*\ln(D+f))+b_2*\ln(H)$.....(1)

Where:

ln = natural logarithm to the base e;

V = stem volume (m^3);

D = Diameter at breast height (cm, over bark);

f = correction factor,

H = Total tree height (m).

In order to estimate volume for the remaining species namely *E. tereticornis, E. urophylla, G. robusta* and *P. kesiya,* which did not have coefficients for volume estimation, the following assumptions were made:

- a tree was assumed to have two parts, a 2 m cylindrical butt log and a conical top portion of (h-2) m length.

- some species were assumed to have similar forms.

In this case, *E. saligna* was assumed to be similar to *E. tereticornis* and *E. urophylla, P. patula* to *P. maximinoi* and *P. tecunumanii* while *P. caribaea* was considered similar to *P. kesiya* and *G. robusta.* All groups of species assumed to be similar were of approximately equal ages.

Total mean tree volume (V) over bark per plot was estimated using the equation

$V=((\pi D^2)/2+\pi D^2 (h-2)/12)$.....(2)

where V = total mean tree volume per plot, under bark (m^3), and

D = diameter at base of cone (also assumed to be equal to diameter at breast height (m)).

A correction factor, cf, taken as the ratio between volumes obtained by using equation 1 to that obtained by using equation 2 for *E. saligna, P. caribaea* and *P. patula* was then multiplied by volumes obtained by using equation 2 for the species assumed to be similar (i.e. the cf of *E. saligna* (0.9605) used for *E. tereticornis* and *E. urophylla,* that of *P. caribaea* (0.8887) for *P.*

kesiya and *G. robusta* and that of *P. patula* (0.7809) for *P. maximinoi* and *P. tecunumanii*) so as to reduce their volumes to under bark values.

Volume estimation by this method may be subject to some errors but was considered satisfactory for the purpose of comparing the performance of the different seed sources in this study since it is applied to all treatments in a uniform manner, and thus unlikely to influence the results.

Heritability was estimated for *E. tereticornis* to study its extent at family level. In this respect, plot means were used for 15 families originating from the species natural range. Due to the fact that the seed sources were open pollinated, and because of the greater propensity for self pollination of *Eucalyptus* species, a coefficient of relatedness of 10/3 was applied (Snedden, 2000).

Heritability was estimated as follows:

$$h^2 = 3.33\sigma_F^2/(\sigma_p^2 + \sigma_F^2)$$

where h^2 = heritability;

σ_F^2 = variance component due to family, and

σ_p^2 = variance component due to plot.

The corresponding standard error for the variance components were estimated by using the following formula (Stonecypher, 1966):

$$V(\sigma^2) = 2/p^2 \sum V_i^2/(f+2)$$

Where $V(\sigma^2)$ = standard error of the variance component;

p = the coefficient for the component being estimated;

V_i = the ith mean square which is used to estimate the component, and

f= the number of degrees of freedom associated with the ith mean square

4. RESULTS AND INTERPRETATION

This chapter presents the results and discussion on the general performance of different species in different trials and seed source variation within the trials as revealed through the analyses of variance and trait-trait correlation in terms of survival, growth and quality traits. It also gives the findings on juvenile-mature correlations for the species at different ages as well as the correlation analysis between performances of the seed sources in terms of growth in relation to the locational variables of the different sources in the sites of origin.

4.1. Overall performance of test species in terms of survival, growth and stem quality characteristics

The overall trial means of different species at last assessment dates in survival, diameter, height, stem form, branching pattern and volume under bark are given in Table 4.1. Of the three *Eucalyptus* species evaluated, *E. urophylla* had performed best followed by *E. saligna,* and *E. tereticornis* in all traits, except in branching pattern where *E. saligna* was the best, followed by *E. urophylla* and *E. tereticornis* (Table 4.1). *E. urophylla* mean growth was about four times and *E. saligna* about three times that of *E. tereticornis.* The three species produced above average trees for stem form and branching pattern, i.e. ranking higher than the mid point of the ranking scale (4/8). The values ranged from 64% (5.44/8) to 79% (6.32/8) in stem form and from 64% (5.44/8 to 81% (6.48/8) in branching pattern of the top rank for *E. tereticornis* and *E. urophylla* respectively. *E. urophylla* had also shown slightly better survival than the other two eucalypt species. *Grevillea robusta* had survival below 50% and also indicated below average branching pattern (3.7/8), but had stem form better than average (4.6/8).

For the pines, although no attempt was made to compare the performance of different species, a general view indicates that, of all the pines evaluated, *P. maximinoi* produced highest volume followed by *P. tecunumanii. P. kesiya* and *P. caribaea* had smallest volume production. Yield of *P. patula* was intermediate between the high yield *P. maximinoi* and *P. tecunumanii* and the poor yield *P. kesiya* and *P. caribaea. P. patula* on site II had given inferior height and superior

diameter growth than on site II. All the pines on average had poor stem form and branching pattern. *P. caribaea, P. kesiya* and *P. patula (*site II) indicated average to slightly below average performance in these traits. *P. tecunumanii, P. maximinoi* and *P. patula (*site I) had indicated poorer performance in that order.

Table 4.1: Trial means indicating species performance in survival, growth, stem form and branching pattern traits of the ten trials at last assessment occasion.

Species	Age (years)	Survival (%)	DBH (cm)	Height (m)	Stem form	Branching	Volume (m^3)$^+$
Eucalyptus saligna	15	45 (5.948)	25.6 (2.057)	27.2 (0.984)	5.5 (0.262)	6.5 (0.239)	0.531 (0.118)
E. tereticornis	15	43 (2.061)	17.6 (0.558)	19.9 (0.388)	5.1 (0.110)	5.1 (0.110)	0.183 (0.002)
E. urophylla	15	59 (6.8)	29.3 (0.25)	28.2 (0.435)	6.3 (0.126)	5.7 (0.234)	0.716 (0.009)
Grevillea robusta	13	41.9 (1.620)	18.2(0.0.353)	19.2 (0.439)	4.6 (0.106)	3.7 (0.145)	0.189 (0.007)
Pinus caribaea	13	89.0 (2.129)	18.7 (0.198)	17.0 (0.215)	4.7 (0.199)	5.4 (0.111)	0.175 (0.006)
P. kesiya	16	44.2 (3.473)	16.8 (0.294)	12.9 (0.240)	4.8 (0.207)	5.0 (0.106)	0.106 (0.003)
P. patula- Gitarama	16	71 (1.601)	23.9 (0.410)	12.8 (0.187)	3.3 (0.120)	2.9 (0.105)	0.205 (0.009)
P. patula-Ruhengeri	15	53 (2.684)	21 (0.329)	17.6 (0.208)	4.7 (0.133)	4.7 (0.165)	0.228 (0.023)
P. maximinoi	14	53 (4.467)	34.2 (1.042)	24.0 (0.706)	3.4 (0.186)	3.5 (0.073)	0.600 (0.046)
P. tecunumanii	14	42 (11.422)	30.3 (1.891)	21.3 (0.787)	4.0 (0.227)	3.9 (0.177)	0.514 (0.067)

Figures in brackets indicate standard error. $^+$ Volume/tree (m^3) (under bark).

The reasons for the observed low volume production by *E. tereticornis* may be due to species interaction with the environmental characteristics of the introduction site. Although the site characteristics are not very different from the optimum ones, the species is said to be sensitive to site quality and silvicultural practices (Eldridge, *et al.*, 1994). The optimum rainfall is reported to be between 800-1500 mm per year, and the species to prefer deep, well drained and fairly light textured soils (Eldridge, *et al.*, 1994). The experimental site receives an annual rainfall of about 1232 mm (Egli and Pietrowicz, 1990) and soils described as shallow and of light texture, with a sandy-clay character at the surface (Gasana, 1973). Also, *E. tereticornis* is known to be a slower grower than *E. grandis* and *E. saligna* and it is generally adapted to drier sites (Eldridge, *et al.*, 1994; Florence, 1996). The experiment received only one thinning in the first ten years. This, together with shallow soil of the site may have influenced the yield. The quality of the seed sources used may also have influenced the results. No information is available on the number of parent trees and whether the sources were natural or man made plantations which would give an idea of the degree of relatedness of the mother trees.

The high yield by the other two *Eucalyptus* species is not unexpected. The growth of *E. saligna* is fast and comparable to that of *E. grandis.* It is reported to perform better than the former in the North Island of New Zealand (Barr, 1983). *E. urophylla* is also reported to be suitable as plantation species in humid and sub humid climates where it has indicated good growth (Eldridge *et al.*, 1994). The performance of *G. robusta* in terms of growth as a plantation species is promising. As already pointed out, the results are better than those reported in Rwandan central plateau ecological zone where the trial is located (Kalinganire, 1996). Yields reported around Mt. Kenya (Kamweti, 1992) and in the highlands of Uganda (Okorio and Peden, 1992) are slightly higher but this may not mean much since site characteristics and treatments may be markedly different.

The observed high volume production by *P. maximinoi* and *P. tecunumanii* is promising. The species have never been tried locally as plantation species. Still they may be among the best plantation species in the country. The poor performance of *P. patula* may be related to site as described in section 4.2. Similarly, the general poor performance of *P. caribaea* and *P. kesiya* may be attributed to site conditions and the silvicultural treatments during the experimental period. The two are planted on shallow, stony soils. The site for *P. kesiya* has lower rains and experiences a comparatively longer dry season of about four to six months a year, while other trials experience a mean dry season of three months.

4.2. Results of the analyses (ANOVA and correlation) for the different species

4.2.1. *Eucalyptus saligna*

4.2.1.1. Seed source variation in survival, growth and quality characteristics in *Eucalyptus saligna*

Eucalyptus saligna showed significant variation in survival, diameter, height and volume growth at age 15 years. Stem form showed variation at younger age (10 years) but this was lost in the

course of growth. Growth traits demonstrated variation only at a later age (15 years) except diameter. This was shown between seed source variation at 10 years (Table 4.2 (a)). Kangaroo River (1) (Australia) followed by Lushoto (2) (Tanzania) sources produced significantly higher volumes and the proportion of the highest to the lowest volume produced is about 3:1 (Table 4.2 (b)). Although not statistically different from other sources, the two sources started showing superior volume production as early as 10 years when the Lushoto source was leading in volume production (followed by Laura River provenance) by 2.4 times the lowest volume producer at the time (the Zomba Plateau, Malawi source). The remaining sources, including the local source, produced volumes that were not significantly different from each other. These were obtained from earlier introductions to Kenya, Malawi and Rwanda, and the origin of these is not known. Although not statistically different, all sources had indicated good stem and branching pattern.

Table 4.2(a): Analysis of variance for *Eucalyptus saligna* trial in Ruhande Arboretum for different traits at four measurement occasions.

Source of Variation	Degrees of Freedom	Age (years)	MEAN SQUARES					
			SURV (%)	DBH (cm)	HEIGHT (m)	STEM	BRANCH	VOLUME (u.b)(m^3)
Block	2	1	382.200	-	0.051	-	-	-
Prov	4		872.767*	-	0.043 ^{NS}	-	-	-
Error	8		190.367	-	0.017	-	-	-
Block	2	2	117.267	9.220	9.432	-	-	0.000010
Prov	4		431.400*	1.941^{NS}	1.842 ^{NS}	-	-	0.000002 ^{NS}
Error	8		105.100	1.177	0.493	-	-	0.000001
Block	2	10	441.267	12.429	1.633	0.313	-	0.090
Prov	4		577.433 ^{NS}	30.62*	5.607 ^{NS}	1.638*	-	0.028^{NS}
Error	8		176.683	7.437	4.460	0.247	-	0.0103
Block	2	15	36.867	17.394	7.994	2.612	43.862	0.0566
Prov	4		539.433*	64.107**	15.276*	1.062 ^{NS}	7.392 ^{NS}	0.2098**
Error	8		95.783	7.511	3.496	0.397	14.392	0.0209

^{NS} provenance means are not significantly different at (P>0.05).*provenance means are significantly different (P <0.05). **provenance means are significantly different (P<0.01).

Table 4.2(b): Mean survival, diameter, height, volume, stem form and branching pattern per provenance of *Eucalyptus saligna* trial in Ruhande Arboretum at different ages.

P	SV2	SV10	SV15	D2	D10	D15	HT2	HT10	HT15	ST10	ST15	BR15	V2	V10	V15
1	42.7b	41.0a	36.7b	3.34a	23.8ab	31.5a	3.34a	22.8a	29.3a	3.28b	5.7a	7.3a	.0032a	.304a	.827a
2	45.0b	38.3a	28.7b	4.76a	24.7a	29.6a	4.56a	22.6a	29.3a	2.40b	5.1a	6.4a	.0047a	.372a	.808a
3	61.0ab	60.0a	43.0ab	2.94a	19.3bc	23.1b	2.61a	23.7a	27.0ab	3.73b	5.6a	6.7a	.0027a	.186a	.400b
4	71.7a	66.7a	60.4a	3.53a	18.0c	22.3b	3.59a	20.0a	23.9b	7.55a	4.9a	5.9a	.0033a	.153a	.330b
5	71.7a	66.7a	57.0a	4.61a	18.3c	21.4b	4.32a	22.6a	25.6ab	3.73b	6.4a	6.2a	.0042.a	.166a	.291b

P = provenance, SV = survival (%), D = DBH (cm), HT = height (m), ST= stem form, BR=branching pattern and V=tree volume (m^3) under bark. The numbers correspond to age of assessment, e.g., HT15 indicates tree mean height as assessed 15 years after planting. Mean values with the same letters are not significantly different at P=0.05 probability level.

The significant variation in seed sources of *E. saligna* indicates the presence of high genetic variation in the species since the trial was very small. This represents a high potential for tree

improvement through breeding. Although no significant differences were found between seed sources in stem form and branching pattern, the fast growing Kangaroo River and Lushoto sources also ranked high. This may eliminate the doubts that the observed high yield is associated with poor survival (low stand density) since, low stand density would be expected to cause poorer tree forms and coarser and heavier branching. This therefore proves superiority of the two sources and their positive interaction with the environment of the study site. The species is known to exhibit seed source variation in other sites. It is reported to have indicated variation in Argentina, with Clifford, Queensland (Australia) outgrowing other sources (Alliani *et al.*, 1991).

4.2.1.2. Age-age correlation in survival and growth traits in *Eucalyptus saligna*

Age-age correlation for *Eucalyptus saligna* in survival was consistently highly significant between one and two, one and 10 and one and 15 years (Table 4.2 (c)). Height growth indicated large but non-significant correlations during the same period. Between two and 10 years, correlations were either small or non-existent for all traits except survival, which had large but non-significant values. Strong correlations were again shown by all traits except height between ages 10 and 15 years. The observed lack of, or less strong correlations between traits may be attributed to trial size with very few degrees of freedom. Large interval between assessments also makes it difficult to tell the juvenile age at which growth would be used in predicting mature tree dimensions.

Table 4.2(c): Age-age correlation in survival and growth traits for *E. saligna* trial in Ruhande Arboretum.

Trait	Age (years)	Trait at age		
		Year 2	Year 10	Year 15
Survival	1	0.88*	0.99***	0.92*
Height	1	0.54^{NS}	0.68^{NS}	0.71^{NS}
Survival	2		0.84^{NS}	0.77^{NS}
DBH	2		0.23^{NS}	0.05^{NS}
Height	2		0.22^{NS}	0.17^{NS}
Volume	2		0.45^{NS}	0.29^{NS}
Survival	10			0.93*
DBH	10			0.96**
Height	10			0.71^{NS}
Volume	10			0.96**

^{NS} provenance means are not significantly different (P>0.05). *Provenance means are significantly different (P <0.05).

****Provenance means are significantly different (P<0.01). *** Provenance means are highly significantly different (P<0.001).**

4.2.1.3. Trait-trait phenotypic correlation in survival and growth characteristics in *E. saligna* at 15 years

E. saligna indicated strong trait-trait correlations between survival and height and survival and volume (Table 4.2 (d)). Volume was strongly correlated with all traits except stem form. Branching pattern also was correlated with both diameter and height traits. The lack of age-age correlation in growth traits between juvenile and mature growth (even up to 15 years in height) may indicate unreliability of diameter and height for prediction of growth and yield in later stages. This agrees with the report that height at the age of one and two years was totally an unreliable predictor of height at 16 and 17 years in *Juglans nigra* and *Fraxinus americana* (Clausen, 1982).

Table 4.2(d): Trait-trait phenotypic correlation in survival and growth traits for *E. saligna* trial in Ruhande Arboretum at 15 years.

N	Trait	Diameter	Height	Stem form	Branching	Volume
5	Survival	0.84^{NS}	0.91*	0.18^{NS}	0.87^{NS}	0.90*
	Diameter		0.84^{NS}	0.22^{NS}	0.96**	0.99**
	Height			0.19^{NS}	0.94*	0.90*
	Stem form				0.03^{NS}	0.15^{NS}
	Branching					0.97**

N=number of observations (seed sources). ^{NS} provenance means are not significantly different (P>0.05)*provenance means are significantly different (P <0.05). **provenance means are significantly different (P<0.01).

The highly significant phenotypic correlation coefficient in volume between 10 and 15 years (Table 4.2c) and the large (but non significant) correlation in height between the same years compare favourably with literature that this relationship is higher in volume than in height in eucalypts in Congo (Bouvet, 1995). The observed strong correlation between over bark diameter and height with under bark volume is not unexpected since the two are used directly in the estimation of volume.

4.2.2. *E. tereticornis*

4.2.2.1. Seed source variation in survival, growth and quality traits in *E. tereticornis*

E. tereticornis showed variation between seed sources in survival at year one and two, but this disappeared with age since it was not observed beyond three years. Height and volume growth did not give a clear picture of variation between seed sources. The variation was observed during juvenile stage (at year one, two and three for height and at year three for volume) (Table 4.3 (a)).

Table 4.3(a): Analysis of variance for *Eucalyptus tereticornis* trial in Ruhande Arboretum for different traits and different assessment occasions.

Source of variation	DF	Age (years)	MEAN SQUARES					
			Surv (%)	DBH (cm)	Height (m)	Stem	Branch	Volume (m^3)
Block	3	1	725.779	-	0.326	-	-	-
Source	16		659.515**	-	0.283*	-	-	-
Error	48		241.477	-	0.146	-	-	-
Block	3	2	254.601	1.939	1.367	-	-	0.0000097
Source	16		548.945*	3.464*	1.319*	-	-	0.0000063^{NS}
Error	48		241.015	0.844	0.637	-	-	0.000044
Block	3	3	-	3.679	2.873	-	-	0.000084
Source	16		-	5.446***	3.678*	-	-	0.000109***
Error	48		-	1.397	1.678	-	-	0.000029
Block	3	6	659.544	9.412	-	-	-	-
Source	16		297.577^{NS}	7.756***	-	-	-	-
Error	48		217.065	1.363	-	-	-	-
Block	3	9	980.738	3.863	9.072	0.840	-	0.00114
Source	16		481.178^{NS}	9.559*	7.527^{NS}	1.801^{NS}	-	0.00119^{NS}
Error	48		266.881	4.437	6.361	1.309	-	0.00109
Block	3	11	269.258	0.998	4.958	8.267	-	0.000651
Source	16		504.502^{NS}	15.656*	10.371^{NS}	1.524^{NS}	-	0.00624**
Error	48		298.652	6.990	5.739	1.476	-	0.00251
Block	3	15	702.995	2.174	3.840	16.811	36.342	0.00605
Source	16		408.454^{NS}	21.244**	10.479^{NS}	1.323^{NS}	0.7312^{NS}	0.016562^{NS}
Error	48		314.631	8.554	7.307	1.402	0.825	0.00959

DF=degrees of freedom. ^{NS} seed source means are not significantly different (P>0.05). *Seed source means are significantly different (P <0.05). ** Seed source means are significantly different (P<0.01). * Seed source means are highly significantly different (P<0.001).**

This was not found at year nine and beyond for height, observed at year 11 and disappeared again at year 15 for volume. Stem form and branching pattern also gave values that were not statistically different between seed sources. Unlike other traits, diameter showed significant differences between seed sources throughout the experimental period. Mean performance of the different seed sources in terms of growth and quality characteristics is given in Table 4.3(b). The lack of significant differences in *E. tereticornis* is not surprising since, although the trial looks big, it actually consists of only five seed sources. Seed sources from Australia are grouped into three sources, that is, two to six, seven to 11 and 12 to 16 may have been obtained from individual trees although this is not specified.

Based on a five seed source (section 3.1.2.2.), it is clear that Laura River sources (12-16) outgrow the other two natural sources (2-6 and 12-16) in terms of volume production. Diameter growth seems to be more sensitive to environment compared to other traits. Since diameter is directly related to yield, Laura River (12-16) (Australia) and Spearhead Farm (1) (Malawi) indicate bigger diameter and thus superior growth under the environmental conditions of this study, although closer experimental control and wider seed source would be needed to demonstrate this.

Although not significantly different, survival of the local source is the highest. It has also outgrown the Halenvale (7-11) and Mount Garnett sources (2-6) sources (both from the species range) and its growth compares favourably with that of superior sources (Table 4.3 (b)). This may partly be due to its adaptability to local environment where it has been growing since early 1900`s (Burren, 1995) and partly due its originating from a plantation. Halenvale and Mt. Garnett sources may have originated from natural forests, where considerable inbreeding may have taken place due to neighbourhood of the parent trees, leading to depressed growth (Eldridge *et al.*, 1994).

A heritability test carried out at family level for diameter, height and volume gave 1.20, 0.72 and 1.02 values respectively and the corresponding errors are 1.32, 0.55 and 0.96 for diameter, height and volume respectively (Table 4.3 (c)). The higher and greatly inflated heritability estimates are reported to occur when provenance differences are incorporated into heritability calculations (William and Matheson, 1994).

Table 4.3(b): Mean survival, diameter, height, volume, stem form and branching pattern per seed source for *Eucalyptus tereticornis* trial in Ruhande Arboretum at different ages.

P	SV1	SV9	SV15	D3	D9	D15	HT1	HT3	HT9	HT15	ST9	ST15	BR15	V3	V9	V15
12	41.8ab	46.0a	37.8a	7.85a	14.08a	21.45a	2.60ab	9.50ab	17.5a	22.2a	6.98a	4.3a	4.3a	0.0218ab	0.110a	0.312a
1	70.8a	41.5a	41.5a	5.98abc	12.77ab	19.43ab	2.40ab	8.78ab	15.9a	22.5a	7.00a	5.1a	5.1a	0.0142ab	0.104a	0.293a
13	87.5a	71.0a	37.8a	7.80a	14.60ab	19.73ab	2.70a	9.30ab	17.8a	20.7a	4.28a	5.5a	5.5a	0.0215a	0.117a	0.268a
14	85.5a	62.5a	52.3a	7.88a	13.58ab	20.40ab	2.70a	9.88a	15.2a	21.0a	6.20a	5.4a	5.4a	0.0222a	0.089a	0.268a
15	85.5a	75.0a	48.0a	6.83ab	11.98ab	19.90ab	2.53ab	9.08ab	15.8a	19.3a	5.50a	5.1a	5.1a	0.0155ab	0.074a	0.239a
16	79.3a	54.3a	54.3a	7.65a	11.13ab	19.75ab	2.50ab	9.10ab	16.9a	20.0a	6.73a	4.4a	4.4a	0.0194a	0.066a	0.239a
17	91.8a	62.5a	58.3a	5.38abc	12.43ab	18.78ab	2.43ab	8.08ab	16.9a	22.0a	6.67a	5.5a	5.5a	0.0090ab	0.088a	0.233a
5	73.0ab	56.3a	37.3a	7.68a	13.55ab	18.45ab	2.30ab	9.30ab	17.4a	21.4a	6.40a	4.6a	4.6a	0.0200a	0.099a	0.220a
7	84.3a	58.3a	37.5a	7.48a	11.98ab	16.98ab	2.19ab	9.28ab	17.3a	20.2a	6.48a	5.5a	5.5a	0.0189a	0.077a	0.178a
2	79.0a	53.8a	29.3a	7.13ab	11.20ab	16.83ab	2.50ab	9.05ab	16.1a	20.3a	6.35a	5.3a	5.3a	0.0168ab	0.065a	0.174a
3	58.5ab	33.0a	33.0a	4.40bc	8.95b	16.43ab	1.85ab	6.80ab	13.9a	19.5a	5.93a	4.8a	4.8a	0.0055b	0.043a	0.164a
6	87.5a	45.8a	45.8a	6.50abc	12.15ab	15.93ab	2.45ab	8.35ab	15.8a	19.0a	5.45a	5.3a	5.3a	0.0135ab	0.074a	0.147a
9	73.0a	58.3a	43.8a	6.30abc	10.83ab	15.40ab	2.23ab	7.85ab	13.9a	18.8a	6.93a	5.4a	5.4a	0.0119ab	0.054a	0.138a
8	77.3a	50.0a	48.0a	6.70abc	10.43ab	15.10ab	2.33ab	8.83ab	17.3a	18.4a	6.05a	4.8a	4.8a	0.0159ab	0.062a	0.134a
4	87.5a	45.8a	33.3a	6.70abc	10.13ab	15.33ab	2.38ab	8.73ab	14.9a	17.9a	5.50a	5.7a	5.7a	0.0145ab	0.050a	0.130a
10	81.3a	68.5a	43.8a	5.95abc	10.90ab	15.55ab	2.33ab	7.60ab	14.8a	17.3a	5.30a	4.9a	4.9a	0.0110ab	0.059a	0.130a
11	62.3ab	55.3a	55.3a	4.05c	10.00ab	13.50b	1.70b	6.32b	13.2a	17.6a	4.90a	4.3a	4.3a	0.0060b	0.043a	0.111a

Values in the same column with same letters are not statistically different (P<0.05) based on SNK test. P=seed source, SV=Survival (%), D=Diameter at breast height (DBH) (cm), HT=Tree height (m), ST=Stem form, BR=Branching pattern and V=Volume (m^3)/tree (under bark). Numbers correspond to year at assessment, e.g. D9=DBH as assessed nine years after planting.

This is however not unexpected since the corresponding standard error values are also large, which may be attributed to the fewer number of families tested. A large number of unrelated individuals is required in order to broaden the genetic base in progeny testing. Eldridge *et al.*, 1994) suggest more than 100 individuals while Shelbourne, (1969) propose a minimum of 200 individuals. The observed large heritability values may imply that selection at family level is possible in this species and that considerable genetic gains could be obtained through selection.

4.2.2.2. Age-age correlation in survival and growth traits in *E. tereticornis*

E. tereticornis showed significantly high correlations as early as between one and two, and three years for survival and diameter respectively and these were maintained throughout the experimental period (Table 4.3 (d)). All juvenile age height values correlated favourably with each other throughout the experimental period except those at years one, three, nine with that at year 11. Volume had indicated no age-age correlation between years two and 15, three and 15, nine and 15 and 11 and 15, but volume at years two and three correlated strongly with those at years nine and 11.

4.2.2.3. Trait-trait phenotypic correlation in survival and growth characteristics in *E. tereticornis* at 15 years

E. tereticornis trial had generally shown weak trait-trait relationships. Only diameter and height, and stem form and branching pattern showed statistically significant correlations (Table 4.3 (e)). Stem form had indicated moderately large correlation coefficients with all other traits but these were not statistically significant. Unlike for *E. saligna,* one and two year diameter and height may probably be successfully used in predicting mature stage diameter and height respectively in *E. tereticornis,* since a strong age-age phenotypic correlation exists (Table 4.3 (d)). The results compare favourably with those obtained in Congo for eucalypt hybrids (Bouvet, 1991). The author reports highly significant correlations in height and circumference of eucalypt hybrids between 20-34 months and 67-80 months with r-values ranging from 0.44 to bigger than 0.90. The strong correlation of juvenile (one to two year) diameter and

height to dimensions at older age (15 years) gives an indication of the opportunity to screen for seed sources, if variation is obtained.

Table 4.3 (c): Estimates of heritability and standard error for growth traits in *E. tereticornis* trial in Ruhande Arboretum.

Trait	Heritability	Standard error
Diameter	1.20	1.32
Height	0.72	0.55
Volume	1.02	0.96

Table 4.3(d): Age-age phenotypic correlation in survival and growth traits for *E. tereticornis* trial in Ruhande Arboretum.

Trait	Age (years)	Trait at age					
		Year 2	Year 3	Year 6	Year 9	Year 11	Year 15
Survival	1	0.82***	-	0.69**	0.75***	0.91***	0.73***
Height	1	0.75***	0.84***	-	0.70**	0.27^{NS}	0.59*
Survival	2	-	-	-	0.55*	0.73***	0.56*
DBH	2		0.73***	-	0.81***	0.56*	0.68**
Height	2		0.76***	-	0.73***	0.60*	0.78**
Volume	2		0.65**	-	0.83***	0.58*	0.13^{NS}
DBH	3			-	0.72**	0.54*	0.56*
Height	3			-	0.81***	0.40^{NS}	0.67**
Volume	3			-	0.68**	0.55*	0.09^{NS}
Survival	6				0.42^{NS}	0.78***	0.74***
Survival	9					0.62**	0.61**
DBH	9					0.72***	0.88***
Height	9					0.40^{NS}	0.74***
Volume	9						0.11^{NS}
Survival	11						0.76***
DBH	11						0.86***
Height	11						0.62**
Volume	11						0.07^{NS}

^{NS} Seed source means are not significantly different (P>0.05) *Seed source means are significantly different (P<0.05) **Seed source means are significantly different (P<0.01). * Seed source means are highly significantly different (P<0.001).**

Genetic correlation can give more reliable results. Results are similar to that reported for *E. grandis* in Colombia (Endo and Easley, 1991) where a recommendation was made that one-year height and volume growth in *E. grandis* can allow for screening new seed lots provided that subsequent evaluation and analysis is undertaken. Under the study conditions, only juvenile diameter and height can possibly be used to predict mature sizes of the same traits since volume is not correlated to them.

Table 4.3(e): Trait-trait phenotypic correlation in survival and growth traits for *E. tereticornis* in Ruhande Arboretum at 15 years.

N	Trait	Diameter	Height	Stem form	Branching	Volume
17	Survival	0.08^{NS}	0.03^{NS}	0.43^{NS}	0.40^{NS}	0.18^{NS}
	Diameter		0.72**	0.33^{NS}	0.05^{NS}	0.11^{NS}
	Height			0.58^{NS}	0.24^{NS}	0.31^{NS}
	Stem form				0.77**	0.21^{NS}
	Branching					0.28^{NS}

N=number of observations (seed sources). ^{NS} Seed source means are not significantly different (P>0.05).

**** Seed source means significantly different (P<0.01).**

4.2.3. *E. urophylla*

4.2.3.1. Seed source variation in growth and quality characteristics

E. urophylla had shown highly significant differences in survival throughout the study period while diameter, height and volume growth had shown significantly different means at three years only (Table 4.4 (a)). All seed sources had survived above 50% and growth characteristics were non significantly different at 15 years (Table 4.4 (b)). Stem form and branching pattern characteristics were not significantly different but higher than average (>60%). As for the *E. tereticornis* trial, the lack of significant correlation in growth and quality characteristics between different seed sources of *E. urophylla* may be attributed to trial size and probably few parent trees from which the seed was collected. Two sources including the local one and the one named unknown (imported from SETROPA, a Netherland`s seed company) do not have full details of their origin. It may not be surprising if they originated from one or two of the tested sources, reducing further the size of the trial to two or three, or from secondary introductions of limited genetic base. Very little variation in different seed sources of *E. urophylla* are reported in South Africa (Clergy and Clarke, 1991) which are attributed to small altitudinal range of the seed sources collected in Flores Island.

Table 4.4(a): Analysis of variance for *Eucalyptus urophylla* trial in Ruhande Arboretum for different traits at different assessment occasions.

Source of Variation	DF	AGE (yrs)	Mean squares					
			Surv (%)	DBH (cm)	Height (m)	Stem	Branch	Volume (m^3)
Block	3	1	1096.083	-	0.0233	-	-	-
Prov	3		1261.083**	-	0.333*	-	-	-
Error	9		146.917	-	0.0720	-	-	-
Block	3	3	852.083	2.341	1.512	-	-	0.0000145
Prov	3		1093.750*	8.994***	5.887***	-	-	0.0000429*
Error	9		156.250	0.218	0.2991	-	-	0.00000549
Block	3	6	811.806	1.254	-	-	-	-
Prov	3		601.389*	25.821^{NS}	-	-	-	-
Error	9		226.667	18.109	-	-	-	-
Block	3	9	712.500	10.029	1.655	0.802	-	0.0171
Prov	3		883.333*	7.807^{NS}	0.495^{NS}	0.064^{NS}	-	0.00801^{NS}
Error	9		176.389	2.846	1.888	1.605	-	0.00313
Block	3	15	197.572	15.47	1.3968	1.3773	1.45706	0.03962
Prov	3		542.404*	1.094^{NS}	2.81139^{NS}	0.09722^{NS}	0.2281^{NS}	0.004779^{NS}
Error	9		72.609	3.897	1.05250	0.19500	0.26713	0.00605086

DF=degrees of freedom, *Provenance means are statistically different (P< 0.05). ** Provenance means are statistically different (P< 0.01). * Provenance means are highly statistically different (P< 0.001).**

Table 4.4(b): Mean survival, diameter, height, volume, stem form and branching pattern per provenance for *Eucalyptus urophylla* trial in Ruhande Arboretum at different ages.

P	SV3	SV9	SV15	D3	D9	D15	HT3	HT9	HT 15	ST 15	BR 15	V3	V9	V15
2	56.3b	53.3b	51.2b	4.3b	24.5a	29.9a	5.1b	23.3a	27.3a	6.2a	5.9a	0.0030b	0.420a	0.730a
3	50.0b	50.0b	50.0b	4.8b	22.9a	29.2a	5.6b	24.1a	29.4a	6.6a	6.2a	0.0037b	0.312a	0.727a
4	87.5a	83.8a	79.0a	7.6a	25.4a	29.3a	7.4a	23.9a	28.0a	6.2a	5.1a	0.0102a	0.471a	0.716a
1	68.8ab	66.3ab	55.5b	4.6b	22.4a	28.6a	4.6b	23.6a	28.1a	6.0a	5.6a	0.0030b	0.366a	0.690a

Figures having the same letters in a column are not significantly different (P>0.05).

P=Provenance, SV=Survival, D=DBH (cm), HT=Tree height (m), ST= Stem form, BR=Branching pattern and V=Tree volume (m^3) (under bark). Numbers correspond to age (years) at assessment.

4.2.3.2. Age-age phenotypic correlation in survival and growth traits in *E. urophylla*

E. urophylla indicated strong age-age correlations only between year one and three, one and nine and three and nine in survival and between year one and three in height (Table 4.4 (c)). Height and diameter showed weak or no correlation at all ages up to nine years and all traits indicated large but non significant correlations at year 15.

4.2.3.3. Trait-trait phenotypic correlation in survival and growth characteristics in *E. urophylla*

E. urophylla indicated no significant trait-trait correlations for all traits (Table 4.4(d)). Diameter and volume and stem form and volume however had considerably large coefficients of correlation (r=0.85 and 0.73 respectively).

Table 4.4(c): Age-age phenotypic correlation in survival and growth traits for *E. urophylla* in Ruhande Arboretum.

Trait	Age (years)	Trait at age			
		Year 3	Year 6	Year 9	Year 15
Survival	1	0.99**	-	0.98*	0.89^{NS}
Height	1	0.99**	-	0.18^{NS}	0.20^{NS}
Survival	3			0.99**	0.92^{NS}
Diameter	3			0.69^{NS}	0.01^{NS}
Height	3			0.11^{NS}	0.29^{NS}
Survival	9				0.94^{NS}
Diameter	9				0.68^{NS}
Height	9				0.90^{NS}
Volume	9				0.41^{NS}

^{NS} Provenance means are not significantly different (P>0.05). *Seed source means are significantly different (P<0.05). **Seed source means are significantly different (P<0.01).

The small size of the trial and the corresponding few degrees of freedom, may have contributed to the observed lack of juvenile-mature as well as trait-trait.

Table 4.4(d): Trait-trait phenotypic correlation in survival and growth traits for *E urophylla* in Ruhande Arboretum.

N	Trait	Diameter	Height	Stem form	Branching	Volume
4	Survival	0.06^{NS}	0.12^{NS}	0.13^{NS}	0.08^{NS}	0.16^{NS}
	Diameter		0.44^{NS}	0.26^{NS}	0.18^{NS}	0.85^{NS}
	Height			0.75^{NS}	0.45^{NS}	0.09^{NS}
	Stem form				0.58^{NS}	0.73^{NS}
	Branching					0.48^{NS}

N=number of observations (seed sources). ^{NS} Provenance means are not significantly different (P>0.05).

The absence of trait-trait correlation is against the report by Clergy and Clarke (1991). that two- and three-year diameter in *E. urophylla* had good correlation with under bark volume. Fairly large phenotypic correlation between stem form and volume (Table 4.4 (d)) may indicate that trees with good forms also have higher yield.

4.2.4. *Grevillea robusta*

4.2.4.1. Seed source variation in growth and quality characteristics in *Grevillea robusta*

The *Grevillea robusta* trial did not show any clear trend in seed source variation in almost all traits. Only height growth had almost maintained variation from year one to 13 but other traits only occasionally showed it (Table 4.5 (a)). All traits had exhibited significant variation at 8 years but it disappeared at 13 years for all except height and branching pattern. It is evident that sources with best height growth namely Imbil (41), Pechey (42) and Coominglan (44) (all from Australia) had also superior branching pattern (Table 4.5 (b)). Being one of the best sources that have shown superior height growth, Benarkin had also indicated best basic wood density at the age of 8 (Table 4.5 (b)).

Table 4.5(a): Analysis of variance for *G. robusta* trial in Ruhande Arboretum for different traits at different assessment occasions.

Source of Variation	DF	AGE (years)	MEAN SQUARES						
			SURV	DBH	HEIGHT	STEM	BRANCH	VOLUME	DENSITY
Block	3	1	20.057	-	0.0398	-	-	-	-
Prov	7		16.215^{NS}	-	0.1025***	-	-	-	-
Error	21		37.861	-	0.0184	-	-	-	-
Block	3	2	36.458	0.168	0.369	3.441	-	0.00000009	-
Prov	7		20.982^{NS}	0.153^{NS}	0.929***	1.344^{NS}	-	0.00000013**	-
Error	21		43.601	0.143	0.105	0.675	-	0.00000003	-
Block	3	5	53.125	1.693	0.634	-	-	0.0000428	-
Prov	7		404.696^{NS}	0.771^{NS}	1.461^{NS}	-	-	0.0000373^{NS}	-
Error	21		198.363	0.836	0.659	-	-	0.00589	-
Block	3	8	7.031	2.026	0.027	0.126	-	0.000743	1.750
Prov	7		219.817*	9.821**	8.628***	1.905*	-	0.00421**	56.857***
Error	21		74.484	1.628	0.448	0.293	-	0.00114	5.250
Block	3	13	79.167	11.034	3.045	3.302	0.230	0.00456	-
Prov	7		83.929^{NS}	3.977^{NS}	6.132*	0.361^{NS}	0.679**	0.00166^{NS}	-
Error	21		98.214	4.085	0.828	0.819	0.151	0.00175	-

DF=degrees of freedom *Provenance means are significantly different (P<0.05). ** Provenance means are significantly different (P<0.01). * Provenance means are significantly different (P<0.001)**

The observed high variation between seed sources of *G. robusta* at eight years and its absence in diameter, stem form and volume traits at 13 years may be a result of the delayed thinning that was done at ten years. Suppression may have accentuated variation to the extent observed at eight years and removal of 30% of the stems reduced it to none in the traits at 13 years. The yield in this trial is better than the general plantation mean volume growth of *G. robusta* reported by Kalinganire (1996)

in the central plateau ecological zone of Rwanda (where the trial is located). He reports a plantation general mean volume per tree of 0.135 m^3 over bark at 12 years.

Table 4.5(b): Mean survival, diameter, height, volume, density, stem form and branching pattern per provenance for *G. robusta* trial in Ruhande Arboretum at different ages.

P	SV5	SV8	SV13	D5	D8	D13	HT5	HT8	HT13	DN8	ST8	ST13	BR13	V5	V8	V13
41	92.5a	83.8ab	45.0a	8.4a	15.9ab	19.5a	9.3a	18.6a	20.0a	489.0c	4.12cd	4.68a	3.98a	.022a	.143ab	.217a
42	97.5a	83.8ab	37.5a	9.2a	16.3a	19.1a	9.8a	17.5b	20.1a	490.3c	5.30ab	4.83a	4.00a	.028a	.155a	.209a
52	90.0a	86.3a	40.0a	8.2a	15.7ab	19.0a	8.9a	16.8b	19.1b	492.8c	5.68a	4.58a	3.20b	.020a	.139ab	.206a
50	72.3a	71.3ab	37.5a	7.8a	14.9ab	18.4a	9.0a	16.6b	19.6a	494.0bc	4.13cd	4.98a	3.48ab	.018a	.122ab	.194a
48	85.0a	80.8ab	37.5a	7.9a	14.7ab	18.0a	9.0a	15.1c	17.4b	490.0c	3.68d	4.18a	3.45ab	.020a	.119b	.184a
44	70.0a	65.0b	42.5a	7.9a	13.6ab	17.3a	8.3a	17.1b	19.2a	429.0c	4.95abc	4.65a	4.45a	.018a	.095b	.172a
46	85.0a	81.8ab	50.0a	8.5a	12.3b	17.2a	9.3a	13.8d	17.2b	497.0ab	4.10cd	4.25a	3.40ab	.023a	.071b	.169a
49	95.0a	83.8ab	45.0a	8.4a	12.3b	16.8a	10.3a	16.4b	20.6a	500.0a	4.43cd	4.98a	3.80ab	.024a	.070b	.163a

Figures with the same letters in the same column are not significantly different P=Provenance, SV=Survival, D=DBH (cm), HT=Tree height (m), ST= Stem form, BR=Branching pattern and V=Tree volume (m^3) (under bark). Numbers correspond to age (years) at assessment, e.g. HT8=Tree height (m) assessed eight years after planting.

This superior growth shown by the different seed sources may indicate the suitability of the test site to *G. robusta.* Imbil (41), Pechey (42) and Coominglan (44) (all from the species` natural range) have shown good height growth and branching characteristics. The first two sources have been collected from reasonably big number of parent trees (10 and 10-20 respectively). The number may support the sources` superiority as it exceeds that of other sources except that of Benarkin (49) and Shyanda (50). Again, Pechey originated from a plantation where the individuals are less likely to be closely related, with the likelihood of reduced inbreeding and its effects on growth (Florence, 1996). Thinning also could lead to the production of superior seed if inferior individual trees are removed. The promising performance of Coominglan source may indicate that it originated from a few superior genotypes since it originates from a very limited number of parent trees in a natural environment. The poor performance of the local source may not be surprising. Its growth may have been affected by the quality and size of the original seed source. Limited introductions from Kenya may account for the lower diversity of the land races in Rwanda (Harwood *et al.*, 1992).

4.2.4.2. Age-age and trait-trait phenotypic correlation for survival and growth traits in *G. robusta*

G. robusta revealed significant age-age correlation in only between year one and two and year five and eight in survival. Both diameter and volume growth indicated strong juvenile-mature correlation only at a later stage (between years eight and 13, Table 4.5 (c)). As for the analysis of variance, height did not give a clear picture of juvenile-mature correlation since it was erratic. It was observed between years one and two and one and five, disappeared between year one and eight and existed again between year one and 13. It was observed again between year five and 13 but not between years eight and 13. Although height growth is known to be less affected by stand density, the observed lack of clear phenotypic correlation may be attributed to lack of thinning. Diameter and volume showed significantly high correlation in *G. robusta* at eight and 13 years (Table 4.5(c)). Stem form at year two also indicated strong correlation with volume at five, eight and 13 years.

It did not however seem to correlate with volume at a later age. Eight-year density highly correlated with four-year diameter and volume and the correlation was negative in both cases. Survival and volume also showed fairly high but non significant correlation (r=0.44). The observed 1-13 year strong correlation in height in *G. robusta* is similar to that reported in *E. grandis* (Clergy and Endo, 1991). It would therefore be possible to utilize one-year height growth in predicting 13-year growth in this species. This is however possible in diameter only at five years since earlier diameter values are not correlated with 13-year diameter.

4.2.5. *P. caribaea*

4.2.5.1. Seed source variation in growth and quality characteristics in *P. caribaea*

The *P. caribaea* trial indicated slight variation in height ($P<0.05$) and stronger variation in stem form and branching pattern ($P<0.01$) (Table 4.6 (a)). Cardwell (4), Queensland (Australia), seed source that had straightest individuals had also the most desirable branching pattern trees and was still among the seed sources observed to produce tallest trees (Table 4.6 (b)).

Table 4.5(c): Age-age and trait-trait correlation matrix for *G. robusta* trial in Ruhande Arboretum at different ages.

Trait	SV2	DBH2	HT2	ST2	SV5	DBH5	HT5	VOL5	SV8	DBH8	HT8	ST8	VOL8	DN8	SV13	DBH13	HT13	ST13	BR13	VOL 13
DBH2	0.36 ^{NS}	1																		
HT2	0.4 0^{NS}	0.89**	1																	
ST2	0.15 ^{NS}	0.18^{NS}	0.07 ^{NS}	1																
SV5	0.31 ^{NS}	0.80*	0.93***	0.07	1															
DBH5	0.15 ^{NS}	0.67 ^{NS}	0.63 ^{NS}	0.18 ^{NS}	0.68	1														
HT5	0.04 ^{NS}	0.70 ^{NS}	0.87**	0.05 ^{NS}	0.81*	0.65 ^{NS}	1													
VOL5	0.16 ^{NS}	0.73*	0.77*	0.09 ^{NS}	0.79*	0.96***	0.81*	1												
SV8	0.40 ^{NS}	0.65 ^{SNS}	0.83*	0.79*	0.92**	0.61 ^{NS}	0.66 ^{NS}	0.68 ^{NS}	1											
DBH8	0.05 ^{NS}	0.32 ^{NS}	0.15 ^{NS}	0.79*	0.16 ^{NS}	0.22 ^{NS}	0.15 ^{NS}	0.13 ^{NS}	0.26 ^{0S}	1										
HT8	0.01 ^{NS}	0.07 ^{NS}	0.01 ^{NS}	0.69 ^{NS}	0.16 ^{NS}	0.19 ^{NS}	0.02 ^{NS}	0.14 ^{NS}	0.01 ^{NS}	0.63 ^{NS}	1									
ST8	0.39 ^{NS}	0.23 ^{NS}	0.13 ^{NS}	0.63 ^{NS}	0.27 ^{NS}	0.44 ^{NS}	0.002 ^{NS}	0.29 ^{NS}	0.20 ^{NS}	0.38 ^{NS}	0.39 ^{NS}	1								
VOL8	0.17 ^{NS}	0.29 ^{NS}	1.01 ^{NS}	0.78*	0.17 ^{NS}	0.26 ^{NS}	0.13 ^{NS}	0.18 ^{NS}	0.20 ^{NS}	0.99***	0.63 ^{NS}	0.40 ^{NS}	1							
DN8	0.44 ^{NS}	0.39 ^{NS}	0.33 ^{NS}	0.85**	0.13 ^{NS}	0.29 ^{NS}	0.46 ^{NS}	0.07 ^{NS}	0.02 ^{NS}	0.82*	0.49 ^{NS}	0.09 ^{NS}	-0.81*	1						
SV13	0.49 ^{NS}	0.54 ^{NS}	0.40 ^{NS}	0.37 ^{NS}	0.13 ^{NS}	0.12 ^{NS}	0.20 ^{NS}	0.11 ^{NS}	0.11 ^{NS}	0.68 ^{NS}	0.30 ^{NS}	0.24 ^{NS}	0.66 ^{NS}	0.67 ^{NS}	1					
DBH13	0.20 ^{NS}	0.24 ^{NS}	0.04 ^{NS}	0.83*	0.23 ^{NS}	0.28 ^{NS}	0.08 ^{NS}	0.20 ^{NS}	0.37 ^{NS}	0.96***	0.62 ^{NS}	0.32 ^{NS}	0.96***	0.96***	0.46	1				
HT13	0.08 ^{NS}	0.40 ^{NS}	0.67 ^{NS}	0.20 ^{NS}	0.68 ^{NS}	0.48 ^{NS}	0.91**	0.65 ^{NS}	0.54 ^{NS}	0.06 ^{NS}	0.27 ^{NS}	0.04 ^{NS}	0.08 ^{NS}	0.34 ^{NS}	0.01 ^{NS}	0.14 ^{NS}	1			
ST13	0.42 ^{NS}	0.03 ^{NS}	0.04 ^{NS}	0.42 ^{NS}	0.12 ^{NS}	0.18 ^{NS}	0.39 ^{NS}	0.22 ^{NS}	0.13 ^{NS}	0.12 ^{NS}	0.63 ^{NS}	0.32 ^{NS}	0.14 ^{NS}	0.24 ^{NS}	0.22 ^{NS}	0.11 ^{NS}	0.65 ^{NS}	1		
BR13	0.13 ^{NS}	0.12 ^{NS}	0.09 ^{NS}	0.13 ^{NS}	0.16 ^{NS}	0.20 ^{NS}	0.07 ^{NS}	0.13 ^{NS}	0.45 ^{NS}	0.02 ^{NS}	0.55 ^{NS}	0.12 ^{NS}	0.01 ^{NS}	0.23 ^{NS}	0.07 ^{NS}	0.09 ^{NS}	0.09 ^{NS}	0.34 ^{NS}	1	
VOL13	0.85**	0.21 ^{NS}	0.01 ^{NS}	0.85**	0.25 ^{NS}	0.29 ^{NS}	0.05 ^{NS}	0.21 ^{NS}	0.38 ^{NS}	0.95***	0.65 ^{NS}	0.34 ^{NS}	0.95***	0.74*	0.44 ^{NS}	0.99***	0.17 ^{NS}	0.15 ^{NS}	0.07 ^{NS}	1

SV=Survival (%), DBH=Diameter (cm), HT=Height (m), ST=Stem form, BR=Branching pattern and VOL=tree volume (m^3) (under bark). Numbers correspond to age (years) at assessment. ^{NS}Correlations between traits are not significant (P>0.05). *Correlations between traits are significantly different (P<0.05) **Correlations between traits are significantly different (P<0.01).*Correlation between traits are highly significantly different. (P<0.001).**

Table 4.6(b): Mean survival, diameter, height, volume, stem form and branching pattern per provenance for *Pinus caribaea* in Kiyombe District at different ages.

PROV	SV1	SV13	D13	HT1	HT13	ST13	BR13	V13
3	97.8a	81.1a	19.7a	0.978ab	18.6a	4.77bcde	5.63ab	0.211a
8	98.9a	96.7a	19.4a	0.993ab	18.0ab	4.84bcd	5.44ab	0.196a
4	98.9a	92.2a	19.5a	1.003a	17.6ab	6.20a	6.09a	0.195a
12	92.0a	70.0a	19.3a	0.918ab	17.1ab	4.24cde	5.04ab	0.193a
10	96.7a	80.0a	19.0a	0.880ab	17.4ab	5.39b	5.90ab	0.188a
6	97.5a	91.3a	19.0a	0.959ab	17.1ab	5.11bc	5.76ab	0.183a
13	100.0a	98.0a	18.5a	0.960ab	17.0ab	5.12bc	5.30ab	0.169a
1	98.8a	90.0a	18.4a	0.924ab	16.9ab	3.39f	4.90ab	0.167a
2	97.8a	94.4a	18.8a	0.930ab	16.2ab	4.39cde	5.19ab	0.165a
7	98.9a	88.9a	18.1a	1.009ab	16.5ab	4.79bcde	5.49ab	0.159a
11	96.7a	88.9a	18.6a	0.818b	15.8b	3.88ef	4.82b	0.156a
9	98.9a	91.1a	17.7a	0.928ab	16.6ab	4.09def	4.92b	0.151a
5	98.8a	93.8a	17.3a	0.906ab	16.2ab	4.46cde	5.30ab	0.143a

Figures having the same letters in a column are not significantly different. PROV=Provenance, SV=Survival (%), D=DBH (cm), HT=Height (m), ST=Stem form, BR=Branching pattern and V=Tree volume (m^3) (under bark). Numbers refer to age (years) at assessment, e.g. V13= Tree volume (m^3) (under bark) at 13 years.

Although over bark diameter at 13 years was highly correlated with volume at 13 years, it is not possible to tell what juvenile diameter-mature volume correlation would have been at an earlier date. Diameter assessment was done only at 13 years and height not more than twice (at one and 13 years).

Table 4.6(c): Age-age and trait-trait matrix for *P. caribaea* trial in Kiyombe District at one and 13 years.

Trait	SV1	SV13	D13	HT1	HT13	ST13	BR13	VOL13
SV1	1							
SV13	0.78**	1						
D13	0.33^{NS}	0.32^{NS}	1					
HT1	0.34^{NS}	0.22^{NS}	0.30	1				
HT13	0.04^{NS}	0.21^{NS}	0.73**	0.60*	1			
ST13	0.29^{NS}	0.12^{NS}	0.41^{NS}	0.56^{NS}	0.47^{NS}	1		
BR13	0.28^{NS}	0.02^{NS}	0.47^{NS}	0.58*	0.56*	0.92***	1	
VOL13	0.26^{NS}	0.40^{NS}	0.94***	0.45^{NS}	0.90***	0.48^{NS}	0.57*	1

^{NS} Seed source means are not significantly different (P>0.05). *Seed source means are significant (P>0.05). **Seed source means are significantly different (P<0.01). ***Seed source means are significantly different (P<0.001).

It might be expected however that the two may be good predictors of mature volume when assessed at earlier stages. Conclusions on this possibility need to be investigated for the species.

4.2.6. *P. kesiya*

4.2.6.1. Seed source variation in growth and quality characteristics in *P. kesiya*

The *P. kesiya* trial revealed strong genetic variation between seed sources in all traits and at all ages, that is, at year one, three, 14 and 16 after planting (Table 4.7 (a)). The source from the Philippines (10) produced highest volume followed by the one from Mugunyana (12) (Zimbabwe) (Table 4.7 (b)). One of the two Columbian sources (3) was the poorest in volume production, followed by the local (11) source from Ruhande Arboretum (Rwanda). The poor volume yielding sources are also characterized by producing individuals with poor stem characteristics.

Table 4.7(a): Analysis of variance for *P. kesiya* trial in Rusumo District for different traits at different assessment occasions.

Source of variation	Degrees of freedom	Age (years)	Mean squares					
			Surv (%)	DBH (cm)	Height (m)	Stem	Branch	Volume (m)
Block	6	1	32.026	-	0.0048	-	-	-
Prov	11		755.174***	-	0.0101***	-	-	-
Error	66		75.925	-	0.00155	-	-	-
Block	6	3	74.329	-	0.0754	-	-	-
Prov	11		716.869***	-	0.489***	-	-	-
Error	66		88.243	-	0.0524	-	-	-
Block	6	14	421.496	5.993	2.578	2.718	-	0.000520
Prov	11		632.055***	8.249***	7.210***	0.950*	-	0.00104***
Error	66		165.959	1.750	1.504	0.389	-	0.000218
Block	6	16	115.200	8.436	1.882	0.908	1.484	0.000542
Prov	11		974.156***	7.459***	4.730*	2.632***	0.871**	0.00105***
Error	66		144.995	2.015	1.678	0.3003	0.309	0.000308

[NS]Provenances are not significantly different (P>0.05). * Provenance means are significantly different (P<0.05). ** Provenance means are significantly different (P<0.01). ***Provenance means are highly significantly different (P<0.001).

Stronger seed source variation is observed in stem than in branching characteristics. Similarly, there is comparatively more variation in diameter and volume than appears to be in height. Similar results are reported on seed source variation and poor performance of the local sources in study sites in different places in this species (Burley and Nikles (1973), Bunvong (1983) and Chuntanaparp *et al.* (1974).

The small sizes of individual trees observed in this trial may be a result of both delayed thinning that was done only at 12 years and poor site quality. Lower rainfall of

the introduction site than that of seed sources may also have contributed to the general poor growth of the trees in the trial. The poor performance of the local seed source may be related to the size of the source (a stand of 0.25 ha in Ruhande Arboretum).

Table 4.7(b): Mean survival, diameter, height, volume, stem form and branching pattern per provenance for *P. kesiya* at Rusumo (Kibungo) site.

P	SV1	SV3	SV14	SV16	D14	D16	HT1	HT3	H14	HT16	ST14	ST16	BR16	V14	V16
10	97.0a	97.0a	56.3abc	35.7d	16.8ab	18.5a	0.62b	2.74ab	13.5a	13.8a	2.27ab	5.00bc	5.06ab	0.109a	0.129a
12	100.0a	96.1a	74.1a	63.3a	16.3ab	17.5a	0.67ab	2.96a	13.6a	14.1a	2.44ab	6.05a	5.33ab	0.105a	0.120ab
8	94.3a	94.3a	60.0abc	44.7abc	17.3a	17.4a	0.66ab	2.74ab	12.9ab	13.5ab	2.57ab	4.71bcd	4.99ab	0.110a	0.115ab
2	99.0a	96.1a	62.9ab	46.7abcd	16.1ab	17.4ab	0.71a	2.57bcd	12.8ab	13.1ab	2.76ab	4.57bcd	4.80ab	0.100a	0.112abc
4	97.1a	95.1a	66.7ab	41.4bcd	15.5ab	17.4a	0.61b	2.39bcd	11.3bc	11.9ab	3.01ab	4.76bcd	5.10ab	0.085ab	0.106abc
1	91.9ab	87.7ab	64.7ab	59.0ab	15.2ab	16.2ab	0.66ab	2.64abc	12.7ab	13.9a	2.06ab	5.80a	5.30ab	0.091ab	0.105abc
6	94.3a	87.6ab	58.7abc	38.1cd	15.9ab	16.9a	0.64b	2.33bcd	11.6abc	12.9ab	2.67ab	4.93bc	5.17ab	0.091ab	0.105abc
5	77.1c	76.1ab	58.4abc	45.9abcd	14.8b	16.7a	0.66ab	2.46bcd	12.0abc	12.4ab	2.54ab	4.57bcd	4.91ab	0.084ab	0.101abc
9	84.6bc	83.6ab	66.9ab	57.3abc	15.3ab	16.4ab	0.65ab	2.66abc	11.9abc	12.9ab	2.06ab	5.46ab	5.59a	0.086ab	0.101abc
7	65.7d	65.7c	41.9c	33.1d	16.0ab	17.1a	0.56c	2.00e	10.8bc	11.5b	2.00b	4.09cd	4.44b	0.086ab	0.100bc
11	97.1a	97.1a	73.4a	45.6abcd	15.7ab	16.0a	0.62b	2.76ab	11.9abc	12.3ab	3.14a	4.69bcd	4.37b	0.091ab	0.094bc
3	98.0a	98.0a	47.6bc	20.0e	13.0c	14.4b	0.68ab	2.27d	10.4c	12.3ab	2.49ab	3.39d	4.79ab	0.067b	0.083c

Figures having the same letters in a column are not significantly different. P=Provenance, SV=Survival (%), D=DBH (cm), HT=Height (m), ST=Stem form, BR=Branching pattern and V=Tree volume (m^3) (under bark). Numbers correspond to years at assessment, e.g. SV14=Survival (%) 14 years after planting.

4.2.6.2. Age-age phenotypic correlation in survival and growth traits for *P. kesiya*

P. kesiya showed significantly high correlation in survival at an early stage (between year one and three) and again at between years 14 and 16 (Table 4.7 (c)). Height indicated strong correlation between three and 14 years. The strong correlation in height growth between three and 14 years may be useful for early selection of best seed sources, provided phenotypic and genetic correlations are related and that the effect of environment on tree growth is low.

4.2.6.3. Trait-trait phenotypic correlation in survival and growth characteristics for *P. kesiya*

For *P. kesiya* trial, the following pairs of traits indicated strong phenotypic trait-trait correlations: survival- stem form, diameter-volume, height-stem form, height-branching pattern and height-volume (Table 4.7 (d); Appendix Table1). Although height-volume correlation was significant, long intervals between measurements (between three and 16 years) is restricting the understanding of juvenile-mature trend in this species. Investigations on other pine species (example *P. oocarpa* in Kenya) report that juvenile-mature correlation is not stable until at five years when provenance superiority emerges (Chagala and Gibson, 1984).

Table 4.7(c): Age-age correlation in survival and growth traits for *P. kesiya* trial in Rusumo District.

Trait	Age (years)	Trait at age		
		Year 3	Year 14	Year 16
Survival	1	0.98***	0.55^{NS}	0.10^{NS}
Height	1	0.42^{NS}	0.36^{NS}	0.52^{NS}
Survival	3		0.50^{NS}	0.02^{NS}
Height	3		0.84***	0.79***
Survival	14			0.74**
Diameter	14			0.85***
Height	14			0.87***
Volume	14			0.92***

^{NS} Provenance means not significantly different (P>0.05). ** Provenance means are significantly different (P<0.01). * Provenance means are significantly different (P<0.001).**

Table 4.7(d): Trait-trait phenotypic correlation for survival and growth characteristics for *P. kesiya* in Rusumo District.

N	Trait	Diameter	Height	Stem form	Branching	Volume
12	Survival	0.28^{NS}	0.55^{NS}	0.87***	0.55^{NS}	0.41^{NS}
	Diameter		0.34^{NS}	0.28^{NS}	0.18^{NS}	0.89***
	Height			0.75**	0.58*	0.71**
	Stem form				0.07^{NS}	0.53^{NS}
	Branching					0.39^{NS}

N=Number of observations (seed sources). ^{NS} Provenance means are not significantly different (P>0.05). *Provenance means are significantly different (P<0.05). ** Provenance means are significantly different (P<0.01). ***Provenance means are significantly different (P<0.001).

This may hold true for *P. kesiya* and probably the stability of the correlation trend be established earlier than the reported five years in *P. oocarpa*, but further studies need to be carried out to ascertain this. Over bark diameter at 14 years was strongly correlated with under bark volume. It is however not possible to predict when diameter started correlating with volume, since the first assessment of the former was only done at 14 years. The strong correlation between diameter and volume and between height and volume is not unexpected since the two are used directly in estimating volume. Similarly, the strong relationship between height and quality traits is not surprising. It implies that trees with good stem form and sparse, small and horizontal branches are normally taller. Trees with big and dense branches are expected to have short boles since more investment is required to develop buttresses or large butt parts that are strong enough to support the heavy branches.

4.2.7. *P. patula*

4.2.7.1. Seed source variation in growth and quality characteristics

The *P. patula* trial at Gitarama (site I) showed highly significant variation between seed sources in all traits except survival at 16 years of age (Table 4.8 (a)). Height demonstrated variation during the juvenile stage (at year one) and maintained it up to 16 years.

Table 4.8(a): Analysis of variance for *P. patula* in Mushubati District (site I) for different traits at different assessment occasions.

SOV	DF	Age (yrs)	Mean squares					
			Surv (%)	DBH (cm)	Height (m)	Stem	Branch	Volume (m^3)
Block	4	1	208.214	-	0.0238	-	-	-
Prov	27		295.529 ^{NS}	-	0.0074**	-	-	-
Error	108		201.548	-	0.0035	-	-	-
Block	4	4	147.705	-	1.751	-	-	-
Prov	27		328.297*	-	0.932***	-	-	-
Error	108		204.151	-	0.309	-	-	-
Block	4	16	356.428	20.529	4.651	1.082	0.807	0.00719
Prov	27		366.561 ^{NS}	23.534***	5.074*	2.032***	1.578***	0.01493***
Error	108		283.095	7.178	2.699	0.456	0.611	0.00506

SOV=Source of variation DF=Degrees of freedom. ^{NS} Provenance means are not significantly different (P>0.05).
Provenance means are significantly different (P<0.05). ** Provenance means are significantly different (P<0.01).
****Provenance means are significantly different (P<0.001).***

The Rancho Thacotha (Mexico) source produced the highest volume followed by DR de Wet FRS (27) from South Africa (Table 4.9 (a)). The two also had significantly higher stem forms and branching patterns. Two South African sources on the other hand, Belfast (18) and Ceylon (16), both from Mpumalanga Province, together with La Venta (6) (Mexico), exhibited the poorest volume production with corresponding poor stem forms and branching patterns. Other African sources also performed well and of all 28 seed sources making the trial, 14 sources ranking high include 10 from African countries.

Apart from branching pattern, the *P. patula* trial in Ruhengeri (site II) did not show any variation between seed sources at 15 years (Table 4.9 (b)). Even height, which

had shown significant variation during young stage (at one year), lost it in the course of growth. The two *P. patula* trials comprise of different seed sources (with some sources common to both trials) and on average, although no differences were revealed between seed sources for the species on site II, it produced taller and straighter trees of comparatively better branching pattern than the trial on site I (Tables 4.9 (a) and 4.9 (b)).

Table 4.8(b): Analysis of variance for *P. patula* in Nyamugali District (site II) for different traits at different assessment occasions.

Source of Variation	Degrees of freedom	AGE (years)	Mean squares					
			Surv (%)	DBH(cm)	Height	Stem	Branch	Volume
Block	2	0+	-	-	0.000269	-	-	-
Prov	11		-	-	0.003427***	-	-	-
Error	22		-	-	0.000600	-	-	-
Block	2	1	0.25000	-	0.0050	-	-	-
Prov	11		1.8864 ^{NS}	-	0.0307***	-	-	-
Error	22		1.3409	-	0.00346	-	-	-
Block	2	15	240.083	0.743	8.941	1.087	0.409	0.00223
Prov	11		262.432 ^{NS}	3.435 ^{NS}	1.599 ^{NS}	0.431 ^{NS}	0.976*	0.00264 ^{NS}
Error	22		182.269	2.930	1.579	0.301	0.390	0.00226

$^{+}$ Seedling height assessed just before planting. ^{NS} Provenance means are not significantly different (P>0.05). *Provenance means are significantly different (P<0.05). * Provenance means are significantly different (P<0.001).**

The high variation in seed sources in terms of growth and quality traits for *P. patula* on site I may partly be attributed to the large size of the experiment and partly due to the variability of the environmental variables of seed origin. The altitudes of the seed source origin range from 945 to 2760 m, an altitudinal difference of 815 m. The seed sources also include some from the species natural range and others from plantations outside the range, where the species may probably have been exposed to much better climatic, silvicultural and soil conditions. Sources from high altitude and higher latitude in South Africa have indicated comparatively worse volume production than low altitude sources. Reasons to this may be the species response to cold conditions, warmer conditions favouring faster growth than colder ones. This may be supported by the following observation. Lower latitude sources from Kenya (2, 14, 16 and 21) and Zimbabwe (12, 13, 17 and 22) compare favourably with low altitude and lower latitude South African sources (20, 24, 25 and 26) (the Kenyan and Zimbabwean sources have warmer temperatures than low altitude and low latitude South African sources).

Table 4.9(a): Mean survival, diameter, height, volume, stem form and branching pattern per seed source for *P. patula* trial in Mushubati District at different ages

PROV	SV1	SV4	SV16	D16	HT1	HT4	HT16	ST16	BR16	VOL16
8	98a	96 a	82a	29.2a	0.514ab	4.54ab	14.4ab	4.7a	3.9ab	0.336a
27	80a	77.5abc	70a	29.0ab	0.496ab	4.30abc	14.0ab	4.5ab	4.1a	0.324ab
3	92a	90 a	78a	26.9abc	0.554a	4.64a	14.1ab	3.6abcde	3.4abc	0.280abc
13	82a	78abc	70a	26.3abc	0.410b	4.08abcd	14.3ab	3.5abcde	3.3abc	0.279abc
12	94a	92a	72a	25.7abcd	0.484ab	4.08abc	15.0a	4.2abc	3.7abc	0.276abc
21	90a	88ab	76a	26.0abcd	0.392b	4.06abcd	13.9ab	4.2abc	3.8abc	0.267abc
17	88a	88ab	78a	24.2abcd	0.518ab	4.28abc	13.5ab	3.1bcde	2.9abc	0.215abc
7	82a	80 a	68a	23.1bcd	0.460ab	3.88bcde	13.2ab	3.0bcde	2.8abc	0.206abc
10	90a	90a	70a	23.9abcd	0.500ab	3.80bcdef	12.6ab	2.4de	2.0c	0.205abc
20	82a	82abc	82a	24.2abcd	0.488ab	3.74bcdef	12.7ab	3.5abcde	3.0abc	0.202abc
25	82a	76abc	72a	23.9abcd	0.498ab	4.12abcd	12.9ab	3.1abcde	2.7abc	0.200abc
19	92a	92a	80a	24.1abcd	0.508ab	4.30abc	12.4ab	3.6abcde	3.1abc	0.200abc
26	82 a	80abc	74a	24.4abcd	0.450ab	3.64cdef	12.4ab	3.0bcde	2.9abc	0.194abc
9	90a	86ab	74a	19.7d	0.462ab	3.66cdef	12.2ab	2.2e	2.0c	0.192abc
14	76	74abc	74a	23.8abcd	0.424ab	3.70bcdef	12.6ab	3.3abcde	2.7abc	0.192abc
1	90a	90 a	82a	23.3abcd	0.522ab	4.20abc	13.0ab	3.9abcd	3.5abc	0.188abc
15	88a	88ab	84a	23.1bcd	0.450ab	3.72bcdef	12.7ab	3.1bcde	3.1abc	0.188abc
24	78a	74abc	64a	24.0abcd	0.482ab	3.52cdef	12.1ab	3.5abcde	3.0abc	0.185abc
5	94a	90 a	66a	23.0bcd	0.502ab	3.80bcde	13.1ab	3.6abcde	3.0abc	0.184abc
11	68a	66bc	54a	22.7cd	0.438ab	3.18ef	12.6ab	3.0bcde	2.7abc	0.181abc
23	80a	78abc	70a	23.3abcd	0.454ab	3.30def	12.1ab	3.3e	2.8abc	0.181abc
22	86a	82abc	58a	22.6cd	0.464ab	3.20ef	12.3ab	2.3e	2.2bc	0.170bc
2	84a	74abc	72a	22.6cd	0.446ab	3.70bcdef	12.2ab	3.0bcde	2.6abc	0.166bc
28	64a	62 c	62a	23.5abcd	0.488ab	4.06abcd	11.5ab	3.2bcde	2.8abc	0.163bc
4	76a	76 a	66a	22.6cd	0.456ab	3.46cdef	11.7ab	2.9cde	2.6abc	0.160bc
16	82a	80abc	70a	21.6cd	0.472ab	3.18ef	11.6ab	3.1bcde	2.8abc	0.146c
6	84a	84 a	62a	20.9cd	0.480ab	3.54cdef	11.7ab	2.4de	2.1bc	0.140c
18	80a	78abc	50a	20.9cd	0.398b	2.98f	10.7b	2.5de	2.2bc	0.121c

Figures having the same letter in a column are not significantly different. PROV=Provenance (seed source), SV=Survival (%), D=DBH (cm), HT=Tree height (m), ST=Stem form, BR=Branching pattern and V=Tree volume (m^3) (under bark). The numbers correspond to age (years) at assessment

Table 4.9(b): Mean survival, diameter, height, volume, stem form and branching pattern per seed source for *P. patula* trial in Nyamugali District at ages one and 15 years.

PROV	SV1	SV15	D15	HT0*	HT1	HT15	ST15	BR15	VOL15
4	100a	60.3a	21.2a	0.317ab	0.94bcd	18.0a	4.73a	4.70ab	0.260a
5	100a	50.0a	21.9a	0.383ab	1.07abc	18.9a	5.53a	5.87a	0.259a
8	98a	58.3a	21.8a	0.370ab	1.08ab	17.4a	4.77a	5.00ab	0.259a
3	98a	44.0a	21.6a	0.407a	1.07abc	17.5a	4.33a	3.90b	0.253a
6	99a	37.7a	22.7a	0.297c	0.88d	17.9a	4.33a	4.47ab	0.248a
11	99a	58.7a	21.0a	0.377ab	1.17a	17.3a	4.23a	4.73ab	0.236a
1	100a	62.7a	20.4a	0.407a	1.13a	17.2a	4.60a	5.17ab	0.229a
9	100a	54.0a	21.0a	0.383ab	0.97bcd	18.2a	4.23a	4.77ab	0.216a
2	99a	64.7a	19.1a	0.360ab	1.05abc	18.0a	5.67a	5.40ab	0.212a
10	100a	52.3a	19.7a	0.370ab	1.06abc	16.5a	4.77a	4.53ab	0.204a
7	100a	37.7a	19.1a	0.353ab	0.92cd	16.3a	4.53a	3.90b	0.195a
12	100a	60.7a	20.1a	0.400a	1.21a	17.7a	4.73a	4.43ab	0.168a

***Height measured just before field planting. Figures having the same letter in a column are not significantly different (P>0.05). PRO=Seed source, SV=Survival (%), D=DBH (cm), HT=Tree height (m), ST=Stem form, BR=Branching pattern and V=Tree volume (m^3) (under bark)**

The performance of sources from the species range in Mexico is variable. Rancho Tacotha (8) that comes from the highest elevation produced the highest volume in the trial. La Venta (6) and Acaxatitlen (4) sources from the lowest sites among the Mexican sources produced significantly less volume than those of the high elevation South African sources under the experimental site conditions.

Although there were no significant correlations between seed source performance and the seed sources locational variables, it seems that the performance of sources from low elevation (2000-2050 m) and high latitude ($20^0$03'N, $98^0$04'W-$20^0$40'N, $98^0$41'W) sites in the Northern Hemisphere compares with that for sources from low elevation (945-1152 m) and high latitude ($24^0$56'S, $30^0$57'E-$25^0$04'E) in the Southern Hemisphere except Rancho Thacotha (8). It is not clear whether the Rancho Thacotha is from an improved source or not, since it behaved differently from other Mexican sources. Collections from South African plantations and from other African sources have given comparable volume yields except the sources from high elevation, cold sites (Belfast (8) and Ceylon (16)) from South Africa; Gisovu (28) from Rwanda and Kinale (2) from Kenya. As would be expected, these have been outgrown by collections from improved source (DR de Wet FRS (27), South Africa). The low production of Staple Ford (17), also an improved source, compared to that of DR de Wet FRS (27) may be due to altitudinal and latitudinal differences (which affect temperature) since the former is on a higher elevation and lower latitude site than the latter.

The trial on site II on the other hand is comparatively smaller, with a relatively smaller altitudinal range and also seed sources collected from the species range alone. The altitudinal range is only from 2000-2500 m. The performance of Mexican sources common to both sites is generally comparable, with a broader range on site I than on site II, probably due to differences in trial site conditions. Although both trials did not receive any thinning, the trees have smaller diameters on site II than on site I probably due to the smaller initial spacing on site II. The initial spacing was 3 m x 3 m and 2.5 m x 2.5 m on site I and II respectively.

Environmental factors of the introduction sites may also have invariably affected the performance of the different seed sources. The trial on site I, which is on a stony, shallower, less fertile and slightly lower elevation with less acidic soils (pH=5-5.5) has developed comparatively shorter, larger individual trees with poorer stem forms and branching characteristics, that are more variable than those on site II trial. The trial on site II on the other hand, which has soils that are deeper, with finer texture and more acidic (pH=4-4.5) compared to the other site, developed taller trees of better stem quality than those on site II. Although it is difficult to conclude here, slight differences in soil acidity may have influenced the tree growth on the trial sites. Pines are reported to be adapted to podzolic soils. These characterized by the existence of the oxides and hydroxides of aluminium and iron, which are acidic in nature (Scholes and Nowicki, 1997).

4.2.7.2. Age-age phenotypic correlation of survival and growth traits for *P. patula*

For *P. patula* on site I, there were strong and consistent juvenile-mature correlations in survival at all ages (Table 4.10 (a)). Height had shown strong correlation between year one and four, none for year one and 16 and highly significant correlation again between year four and 16. Similar observation was made in this study in *P. kesiya*, where there was no significant correlation between years one- and 16-year height but height at year three correlated strongly with that at year 16. The lack of correlation in one year height to that at 16 years, and the observed strong correlation between four-year height and 16-year height growth on site I is again similar to that observed in Kenya on *P. oocarpa* that juvenile-mature correlation is not stable until at five years when provenance superiority emerges (Chagala and Gibson, 1984). Like for *P. kesiya,* the possibility of selecting superior seed lots can be possible at four years in this species. The *P. patula* on site II was assessed only twice (at year one and 15) and only height was measured in both occasions. There was no correlation between height at year one and that at year 15 (Table 4.10 (a)).

4.2.7.3. Trait-trait correlation in survival and growth characteristics for *P. patula*

P. patula trial on site I indicated highly significant correlations between all traits (Table 4.10 (b)). The species on site II showed significantly different but comparatively less strong trait-trait correlations. Only the following pairs of traits indicated strong correlations: diameter and height, diameter and volume, height and branching pattern and stem form and branching pattern (Table 4.10 (c)).

Table 4.10(a): Age-age phenotypic correlation in survival and growth traits for *P. patula* trial on sites I.

Trait	Age (years)	Trait at age	
		Year 4	Year 16
Survival	1	0.96***	0.54**
Height	1	0.55**	0.26^{NS}
Survival	4		0.56**
Height	4		0.73***

^{NS} Provenance means are not significantly different (P>0.05). ** and * Provenance means are significantly different (P<0.01and P<0.001 respectively).**

Table 4.10(b): Trait-trait phenotypic correlation in survival and growth for *P. patula* on site I.

N	Trait	Diamete	Height	Stem form	Branching	Volume
28	Survival	0.41*	0.5**	0.47*	0.48**	0.43*
	Diameter		0.79***	0.82***	0.83***	0.96***
	Height			0.70***	0.75***	0.90***
	Stem form				0.97***	0.80***
	Branching					0.82***

N=number of observations (seed sources). *Provenance means are significantly different (P<0.05). Provenance means are significantly different (P<0.01). *** Provenance means are highly significantly different (P<0.001).**

Table 4.10(c): Trait-trait and age-age phenotypic correlation matrix for *P. patula* trial at site II.

Trait	HT1	SV15	D15	HT15	ST15	BR15	V15
HT1	1						
SV15	0.34^{NS}	1					
D15	0.27^{NS}	0.23^{NS}	1				
HT15	0.07^{NS}	0.22^{NS}	0.62*	1			
ST15	0.03^{NS}	0.23^{NS}	0.06^{NS}	0.43^{NS}	1		
BR15	0.10^{NS}	0.54^{NS}	0.20^{NS}	0.62*	0.70*	1	
V15	0.25^{NS}	0.10^{NS}	0.79**	0.41^{NS}	0.06^{NS}	0.30^{NS}	1

HT=Tree height (m), SV=survival (%), D=DBH (cm), ST=Stem form, BR=Branching pattern and V=Tree volume (m^3) (under bark). Numbers 1 and 15 refer to age (years) at assessment. ^{NS} Coefficients are not significantly different (P>0.05). *Coefficients are significantly different (P<0.05). **Coefficients are significantly different (P<0.01).

The high correlation observed on site I may have been accentuated by the very high variation observed between seed sources since this was higher on site I than on site II. Trial size may have influenced the correlations.

4.2.8. *P. maximinoi*

4.2.8.1. Seed source variation in growth and quality characteristics for *P. maximinoi*

In *P. maximinoi*, all except height and stem form at 14 years traits did not reveal any significant differences (Table 4.11 (a)). The growth for the species on the site is highly promising as indicated by very high provenance mean diameter, height and volume (Table 4.11 (b)).

Table 4.11(a): Analysis of variance for *P. maximinoi* trial in Musebeya District for different traits at different assessment occasions.

SOV	DF	Age (years)	Mean squares					
			Surv (%)	DBH(cm)	Height (m)	Stem	Branch	Volume (m^3)
Block	4	3	-	0.071	0.111	0.067	-	-
Prov	4		-	0.275^{NS}	0.255^{NS}	0.046^{NS}	-	-
Error	16		-	0.270	0.175	0.031	-	-
Block	4	15	301.500	30.138	2.981	0.507	0.933	0.0154
Prov	4		499.000^{NS}	27.243^{NS}	12.817*	0.913*	0.133^{NS}	0.0537^{NS}
Error	16		300.250	17.038	2.913	0.225	0.456	0.0207

^{NS}Provenance means are not significantly different (P>0.05). *Provenance means are significantly different (P<0.05).

Generally, the performance in stem and branch characteristics are not good, but trees performed comparatively better in stem form than in branching characteristics. Santa Jeronima (3) had best mean performance in both height and stem form while Santa Rosita (1) indicated poorest mean performance in the two traits. The lack of variation in most of the traits between seed sources in *P. maximinoi* may be attributed to the small trial size. The high volume production however indicates the suitability of the species to the site.

4.2.8.2. Age-age and trait-trait phenotypic correlation of survival and growth traits for *P. maximinoi*

P. maximinoi indicated fairly high but non significantly different juvenile-mature correlations in diameter and height (the only tested traits) between three and 14 years (Table 4.11 (c)). In all traits, *P. maximinoi* showed strong correlation only between

diameter and volume and height and volume (Table 4.11 (c)). There were no correlations between survival and stem form and height and branching pattern.

Table 4.11(b): Mean survival, diameter, height, volume, stem form and branching pattern per provenance for *P. maximinoi* trial in Musebeya District at different ages.

PROV	SV14	D3	D14	HT3	HT14	ST3	ST14	BR14	V14
3	62a	3.14a	36.4a	3.00a	25.2a	2.82a	4.10a	3.68a	0.717a
2	56a	2.84a	36.5a	2.80a	23.4a	2.90a	3.42ab	3.54a	0.656a
5	38a	3.14a	33.4a	3.14a	24.9ab	2.86a	3.32ab	3.30a	0.606a
4	60a	2.96a	33.9a	3.26a	23.8ab	2.66a	2.96ab	3.30a	0.581a
1	47a	2.58a	30.9a	2.72a	21.2b	2.74a	3.32b	3.44a	0.440a

Figures with the same letters in a column are not significantly different (P>0.05). PROV=provenance (seed source), SV=Survival (%), D=DBH (cm), HT=Tree height (m), ST=Stem form, BR=Branching pattern and V=Tree volume (m^3) (under bark). Numbers 3 and 14 refer to age (years) at assessment.

Table 4.11(c): Age-age and trait-trait correlation for survival and growth traits in *P. maximinoi* trial in Musebeya District.

Trait	D3	HT3	ST3	SV14	D14	HT14	ST14	BR14	V14
D1	1								
HT1	0.72^{NS}	1							
ST1	0.31^{NS}	0.30^{NS}	1						
SV14	0.08^{NS}	0.08^{NS}	0.35^{NS}	1					
D14	0.55^{NS}	0.12^{NS}	0.48^{NS}	0.60^{NS}	1				
HT14	0.99*	0.66^{NS}	0.38^{NS}	0.15^{NS}	0.67^{NS}	1			
ST14	0.55^{NS}	0.18^{NS}	0.62^{NS}	0.03^{NS}	0.44^{NS}	0.57^{NS}	1		
BR14	0.05^{NS}	0.51^{NS}	0.34^{NS}	0.55^{NS}	0.60^{NS}	0.14^{NS}	0.66^{NS}	1	
V14	0.78^{NS}	031^{NS}	0.49^{NS}	0.47^{NS}	0.95*	0.86*	0.60^{NS}	0.53^{NS}	1

D=DBH (cm), HT=Tree height (m), ST=Stem form, BR=Branching pattern and V=Tree volume (m^3) (under bark). ^{NS}Correlations are non significant (P>0.05). *Correlations are significantly different (P>0). The numbers 1 and 14 refer to age (years) at assessment.

Stem form and branching pattern, however, had large correlation coefficients between them and volume but these were not significant due to the low number of degrees of freedom. Fairly large but non significant age-age correlation also may be a result of the small trial size (few degrees of freedom). This is also indicated by the level of significance, where only very large coefficients (r>0.90) are significant (P=0.05). As for the previous trials, although diameter correlated with volume, big interval between measurements is making it impossible to tell at what juvenile age the correlation may have emerged.

4.2.9. *P. tecunumanii*

4.2.9.1. Seed source variation in growth and quality characteristics for *P. tecunumanii*

P. tecunumanii showed significant differences in survival at both juvenile and mature ages. Height and stem form showed between seed source differences at four years but these disappeared in the course of growth, as they were not revealed at 14 years (Table 4.12 (a)). Diameter maintained variation up to 14 years. Volume production indicated slight but significant differences ($P<0.05$) at 14 years (Table 4.12 (a)). The sources from Guatemala (1, 2 and 5) were significantly better than those from Nicaragua (3 and 4) and volume production by the best source in this trial was twice as much as that of the poorest at 14 years (4.12 (b)). For *P. tecunumanii*, the high seed source variation observed may originate from altitudinal differences in the sites of seed origin.

Table 4.12(a): Analysis of variance for *P. tecunumanii* trial in Musebeya District for different traits at different assessment occasions.

Source of Variation	Degrees Of freedom	Age (years)	Mean squares					
			Surv	DBH	Height	Stem	Branch	Volume
Block	4	4	233.500	0.477	0.038	0.274	-	-
Prov	4		2896.00***	14.616**	4.812***	0.960**	-	-
Error	16		271.000	2.264	0.524	0.147	-	-
Block	4	14	196.000	5.445	5.623	0.238	0.493	0.027
Prov	4		3236.000***	74.693 *	11.617^{NS}	1.341^{NS}	0.603^{NS}	0.103*
Error	16		338.000	22.116	5.817	0.942	0.227	0.032

^{NS} Provenance means are not significantly different (P>0.05). * Provenance means are significantly different (P<0.05). ** Provenance means are significantly different (P<0.01). * Provenance means are significantly different (P<0.001).**

Sources from Guatemala themselves had elevations far higher (1800 m, 2000-2200 m and 2300-2600 m), by about twice those from Nicaragua (900 m and 1200 m). The seed source with 1800 m altitude performed best, which may lead to the thinking that the conditions of the site may be comparable to those at the introduction site, at an elevation of 2400 m. This may be supported by the observation that lower elevation sites (Nicaraguan) (3 and 4) as well as higher elevation originating sources (1 and 2) indicated lower volume production (Table 4.11 (b)) than the source at 1800 m altitude. Although also probably affected by latitude and species, altitudinal related

provenance variation is reported to exist in other species but with low altitude originating provenances outgrowing high altitude originating sources. Example, better seedling growth was reported for those originating from lower elevation than those from higher elevation in *P. contorta* (Rehfeldt and Wyckoff, 1981). *E. urophylla* demonstrated high differences in growth between low- and high-altitude sources on some wet tropical sites, with low altitude originating sources outperforming the high altitude originating sources (Eldgridge *et al.*, 1994).

Table 4.12(b): Mean survival, diameter, height, volume, stem form and branching pattern per seed source for *P. tecunumanii* trial in Musebeya District at different ages.

PROV	SV4	SV14	D4	D14	HT4	HT14	ST4	ST14	BR14	V14
5	72a	62a	10.20a	34.5a	4.32ab	23.3a	2.28a	4.32a	3.96a	0.707a
2	76a	72a	10.68a	32.8ab	3.72b	22.8a	2.42a	3.72a	3.64a	0.578b
1	36b	26bc	9.56a	32.8ab	4.58a	21.2a	2.36a	4.58a	3.68a	0.559ab
4	20b	10c	6.36b	25.8b	4.17ab	19.0a	1.52b	4.17a	4.60a	0.375c
3	60a	40ab	8.58a	25.7b	3.30b	20.4a	1.0b	3.30a	3.74a	0.353c

Figures within the same column having the same letter are not significantly different (P>0.05).

PROV=provenance (seed source), SV=Survival (%), D=DBH (cm), HT=Tree height (m), ST=Stem form, BR=Branching pattern and V=Tree volume (m^3) (under bark). Numbers 4 and 14 refer to age (years) at assessment.

4.2.9.2. Age-age and trait-trait phenotypic correlation in survival and growth traits *P. tecunumanii*

The *P. tecunumanii* trial was assessed only twice and juvenile-mature correlation was significant for survival and height (Table 4.12 (c)). The *P. tecunumanii* trial indicated high to very high correlation coefficients between different traits but only strongly significant ones were observed between juvenile diameter and juvenile as well as mature height, juvenile and mature height and between diameter and volume and height and volume at 14 years (Table 4.12 (c)). Correlations between branching pattern and volume, and stem form and volume were the weakest. Similar observations as for *P. maximinoi* in age-age correlation were found in *P. tecunumanii.* This may be due to the size of the trials. The stronger correlation that existed between diameter and volume, and between height and volume at 14 years can be utilized in predicting future yield for the species. It is again difficult to establish when the juvenile-mature correlations emerged due to very limited number of measurements.

Table 4.12(c): Age-age and trait-trait phenotypic correlation matrix for survival and growth traits for *P. tecunumanii* trial in Musebeya District.

Trait	SV4	D4	HT14	ST4	SV14	D14	HT14	ST14	BR14	V14
SV4	1									
D4	0.82^{NS}	1								
HT4	0.77^{NS}	0.99***	1							
ST4	0.52^{NS}	0.89*	0.93*	1						
SV14	0.99**	0.84^{NS}	0.80^{NS}	0.58^{NS}	1					
D14	0.50^{NS}	0.83^{NS}	0.87^{NS}	0.95*	0.54^{NS}	1				
HT14	0.85^{NS}	0.94*	0.93*	0.84^{NS}	0.87^{NS}	0.87^{NS}	1			
ST14	0.42^{NS}	0.02^{NS}	0.11^{NS}	0.43^{NS}	0.37^{NS}	0.55^{NS}	0.11^{NS}	1		
BR14	0.66^{NS}	0.83^{NS}	0.81^{NS}	0.64^{NS}	0.64^{NS}	0.49^{NS}	0.60^{NS}	0.23^{NS}	1	
V14	0.56^{NS}	0.78^{NS}	0.81^{NS}	0.87^{NS}	0.58^{NS}	0.97*	0.90*	0.53^{NS}	0.36^{NS}	1

SV=survival (%), D=DBH (cm), HT=Tree height (m), ST=Stem form, BR=Branching pattern and V=Tree volume under bark (m^3). The numbers 1 and 14 refer to age (years) at assessment. ^{NS} Correlation coefficients not significantly different (P>0.05). * Correlation coefficients are significantly different (P<0.05). **Correlation coefficients are significantly different (P<0.01). ***Correlation coefficients are highly significantly different (P<0.001).

4.3. Correlation between seed source performance and locational variables

No significant correlation was found between seed source mean growth and locational variables of the seed origin performance in diameter and height growth and altitudes and latitudes of seed source origin (Table 4.13 and Appendix Table 1).

Table 4.13: Correlation matrix for seed source mean growth and locational variables of seed source origin for selected trials (*Pinus kesiya* and *P. patula* on site I).

Species	Trait	Seed source locational variables							
		Lat	Long	Alt	Adlat1	Adlat2	Adlat3	Adlat4	Adlat5
P. kesiya	DBH	-0.3105^{NS}	-0.1123^{NS}	0.0522^{NS}	-0.2907^{NS}	-0.3007^{NS}	-0.3040^{NS}	-0.3056^{NS}	-0.3085^{NS}
P. kesiya	Height	-0.2463^{NS}	-0.2951^{NS}	-0.0686^{NS}	-0.2422^{NS}	-0.2445^{NS}	-0.2452^{NS}	-0.2455^{NS}	-0.2460^{NS}
P. patula	DBH	0.1938^{NS}	-0.2540^{NS}	-0.0057^{NS}	-0.1187^{NS}	-0.0769^{NS}	-0.0182^{NS}	0.0451^{NS}	0.1087^{NS}
P. patula	Height	-0.0085^{NS}	-0.0701^{NS}	-0.2552^{NS}	0.0519^{NS}	0.0573^{NS}	0.0589^{NS}	0.0542^{NS}	0.0502^{NS}

Adlat=adjusted latitude. ^{NS} Figures are not significantly different.

The use of adjusted latitudes (refer to section 3.3) did not improve the relationship either (Table4. 13). The lack of correlation between seed source performance in growth and the locational variables of seed source origin was not unexpected. Even in Europe where the idea was first developed, the trend was evident in the north, where altitude is generally not very high. In southern regions of Europe there was no correlation observed and this was attributed to altitude (Wiersma, 1963).

The results are consistent with reports in literature in *P. patula* where provenances did not show any particular altitudinal and latitudinal gradient in Argentina (Barrett, 1977). Comparable results were obtained by Darrow (1983) in South Africa, where only non significant relationships were found between height growth and basal area of *Eucalyptus camaldulensis* and *E. terticornis* and the seed source locational variables. The use of adjusted latitudes by Darrow gave poor to fair relationship and he concluded that their use may not be suitable in the Southern Hemisphere and that the conversion factor of 100 m of altitude to 1^0 of latitude is not likely to hold in the tropical and subtropical conditions. The picture may even be more complicated with planting sites near the equator. This general conclusion was made based only on the work done within an latitudinal range of $24^0$36'S, $30^0$54'E-$26^0$14'S, $30^0$31'E and an altitudinal range of 808-1888 m. Altitudinal variation at the equator may have a very strong influence on species growth, as was found by Kalinganire in *Grevillea robusta* in Rwanda (1992).

5. DISCUSSION AND CONCLUSION

As demonstrated by most of the species studied in field trials, genetic variation between seed sources does exist, as observed even in very small trials of only five seed sources such as those of *E. saligna* and *P. tecunumanii.* Between seed source variation indicates the potential for tree improvement through breeding. The observed age-age and trait-trait phenotypic correlations in some species also demonstrate the possibility of using early tree dimensions in predicting mature growth and early selection of superior seed lots, both of which are useful in tree improvement programmes. This however is commonly done based on genetic and not phenotypic correlations, although the latter can be an indication of the former, especially in species with restricted natural and less heterogeneous ranges. Such species are said to exhibit less genetic-environmental interaction. The importance of this to Rwanda is obvious. Rwanda being a very small country has limited areas for plantation forestry. It therefore requires a strategic breeding programme that will focus on both production and developmental aspects and effectively use the area available so as to meet the increasing demand for wood and wood products. Species selection and identification of the best seed sources that match with the planting sites constitute a primary step in any breeding programme.

Hardwood species are very important in Rwandan plantation forestry. About 97% of national energy consumption is obtained from wood (MINAGRI, 1998) and almost all wood fuel comes from hardwood species. Likewise, wood for construction and poles are also obtained from hardwood species. Market preference for sawn wood and furniture is generally higher for hardwood than for softwood species. Timber from softwood species is mainly used for furniture, veneer and match production, light construction as ceiling boards and packaging, and for the production of other wood based products.

Due to short supply of timber from plantations as well as peoples` preference to hardwood timber, natural forests are getting over-exploited with time. Logging and the conversion of natural forests into agricultural fields through anthropogenic activities have a serious effect on environmental and genetic conservation. The decline of tree populations through selective felling where best individual trees are

cut leads to genetic erosion. This results in loss of genetic diversity, or an unfavourable change in the frequency of adaptive or commercially important alleles (O'Neil *et al.,* undated). Continued selective logging and the resulting over-harvesting reduces tree numbers to critical levels, which may lead to reduced gene flow, resulting in genetic drift, inbreeding depression and lowering of genetic diversity (Murawski and Hamrick, 1991; Murawski *et al.*, 1994). Forest fragmentation also leads to genetic erosion (Hall *et al.*, 1996). Changes in natural forests environment resulting from selective felling as well as the associated disturbances may have considerable effects on species diversity. Extinction of useful or potentially useful species has direct impact on the well being of human communities around the forests. The overall outcome is the endangering of the economic sustainability of the rural communities.

Plantation forestry through introduction of appropriate species and seed sources may have a remarkable contribution to the satisfaction of demand for wood and wood products as well as the conservation of natural forest ecosystems and their plant genetic resources. This would also contribute to the sustainable utilization of the natural forests and ensure their availability for use in future generations.

Of the four hardwood species tested namely *E. saligna, E. urophylla, E. tereticornis* and *G. robusta*, *E. saligna* and *E. urophylla* indicated very high potential as plantation forestry species owing to their very high growth rates as well as quality stems. Although the species are reported to have high yields in other areas in the tropical and subtropical conditions (Eldridge *et al.*, 1994), none of the reported yields is comparable to that obtained under this study, except for *E. urophylla* at Mangombe (Cameroon), where the growth obtained (83 m^3/ha/year) from a low altitude (30 m) source was very high (Eldridge *et al.*, 1994).

E. saligna is reported to have a mean annual increment (MAI) in volume growth of 23.7 m^3/ha/year in South Africa at 14 years (Poynton, 1979). The growth rate obtained under this study varies between seed sources, ranging from 14.7-41.7 m^3/ha/year, with an average of 26.8 m^3/ha/year at 15 years. *E. urophylla* indicated a

very high growth rate, with MAI ranging from 45.6-48.2 m^3/ha/year (47.3 m^3/ha/year on average) at 15 years. The growth reported for this species in other places is lower than this obtained here. *E. urophylla* grown near Edea (Cameroon) had a growth rate of 30 m^3/ha/year at five years, while that in Louduma (Congo) at the same age had 40 m^3/ha/year (Eldridge *et al.*, 1994). The species indicated a growth of 46 m^3/ha/year in a four years stand in South Africa (Poynton, 1979). The very high growth rates for the two species indicate a high potential and therefore are considered appropriate plantation species in Rwanda.

Based on the results of this study, Kangaroo River (1) (Australia) and Lushoto (2) (Tanzania) sources may be recommended for afforestation purposes under the environmental conditions of the study site for *E. saligna.* In order to broaden the genetic base, other sources like Masaita (3) (Kenya) and new sources from the species natural range may be used. Although juvenile (one and two year) height and diameter demonstrated to be poor predictors of 15 year-height and diameter, diameter at 10 years can be used to predict diameter at 15 years and probably older ages. Again, since diameter, height and branching pattern are strongly related to volume at 15 years, selection for high yield could possibly be done based on these traits.

The growth of the local source of *E. urophylla* compares favourably with the imported sources. Since it has been used locally in afforestation programmes for a long time, it should be used together with the imported sources so as to broaden the genetic base. Selection among the existing populations could probably give better results and the use of cuttings may speed up the gains expected from the selected families.

E. tereticornis has proved to be poorly adapted to the conditions of the trial and similar sites. However, MAI obtained under this study (7.9-22.4 m^3/ha/year, with an average of 15.2 m^3/ha/year) is within the range reported in India, which ranged from 2.3-40 m^3/ha/year (Chaturvedi, 1973). The species is reported to originate from a summer rainfall area and adapted to more severe droughts than those of its natural range (Florence, 1996). Based on the current results, the species is not appropriate as a plantation species under the environmental conditions of the trial site. Since it has

been in use in the country for a long time, it can still be used but on low elevation and drier sites. It is reported as one of favoured species in southern lowlands of Nepal (White, 1987). Crossing it with other eucalypt species can be considered so as to develop more useful hybrids. It is said to hybridise naturally with *E. alba, E. grandis* and *E. camaldulensis* and large gains are reported to have been obtained in Congo through mass propagation of the hybrids (Van Wyk, 1985; Eldridge *et al.*, 1994).

Although there was no significant variation between seed sources observed for the species, selection at family level might allow for genetic improvement since considerable variation was observed between families as indicated by high heritability values in growth traits. The imported sources and promising land races from other African countries, including selections from local populations can be used to establish base populations for breeding and seed production. New introductions covering a wider distribution may contain more variation and probably lead to considerable genetic gains.

Grevillea robusta indicated a poor growth rate in this study, where it had a MAI of 14.2 m^3/ha/year at 13 years. The species is reported to be an agroforestry tree species in African agroforestry systems (Neumann, 1983; Poulsen, 1983). They suggest that the species is popular with farmers because it interferes relatively little with the food and cash crops, while at the same time, it produces valuable poles, saw logs and firewood. Tolerance of the tree to side pruning and pollarding, with its leaves used for mulching, makes it an important agroforestry species. A general low yield shown by *G. robusta* in this study may probably be due to unfavourable site conditions. The species performs better when grown under dry conditions (Kalinganire, 1992; Harwood and Owino, 1992). The trial has had only one thinning during the first ten years, which may have contributed to low diameter growth and poor volume production.

As there were no differences between seed sources observed at 13 years, sources from Australia together with the local one, may be used for planting so as to broaden the genetic base. Recent isozyme studies on natural populations and land races confirm

that land races originated from very limited introductions (Harwood, *et al.*, 1992). The authors suggest that, although the genetic bases of the land races appear very limited, selections can still be made from local populations, of which very large ones now exist. Selection in *G. robusta* can be based on height and branching characteristics since these two traits indicated significant differences between seed sources in this study. Eight-year diameter growth can be used to predict 13-year diameter and volume since these are significantly correlated to each other while two-, five- and eight-year heights indicated to be poor predictors of 13-year height. Care must be taken when selecting for volume in *G. robusta* so as not to affect wood density, as the two traits were observed to be strongly negatively correlated. The negative correlation however was only observed at eight years and not at 13 years.

For the pines, growth rates of *P. maximinoi* and *P. tecunumanii* were very high. *P. maximinoi* produced mean annual increment varying between seed sources and this ranged from 28.0-45.6 m^3 of wood/ha/year, with a mean of 38.2 m^3/ha/year at 14 years. *P. tecunumanii* also showed a high growth rate but less than that of *P. maximinoi* at the same age. Its growth ranged from 17.7-35.6 m^3/ha/year between seed sources with an average of 25.9 m^3/ha/year. *P. patula* ranked the third in volume production, with a growth rate of 16.6 m^3 and 20.1 m^3 of wood/ha/year on site I at 16 years and on site II at 15 years respectively. The production of the best seed sources for the first two species was more than twice the volume of the best *P. patula* seed sources on site I and about 1.5 times the growth on site II, irrespective of the fact that the latter is a primary commercial plantation species in use, with some improved sources of *P. patula* being included in the trial. Although the trials were located on different sites, it is believed that the differences in volume production between these species and *P. patula* (the control) are not due to differences in site conditions but the superiority of the other species.

The results are consistent but far higher than that reported for the above mentioned *P. maximinoi* in Colombia and in South Africa, where the its growth rate was superior to that of commercial species (Gapare, 2000). In Colombia, *P. patula* (a primary commercial species) indicated a growth rate of 20 m^3 of wood/ha/year while unimproved *P. maximinoi* averaged 25 m^3 of wood/ha/year, a 20% difference. The

top third of *P. maximinoi* families from the best provenances (representing an improved or adapted population) averaged 41 m^3 of wood/ha/year, a growth rate twice that of *P. patula.* In South Africa, *P. patula* (also a primary commercial species) averaged 12 m^3 of wood/ha/year, while unimproved *P. maximinoi* averaged 14 m^3 of wood/ha/year, a 17% difference. The top third of the *P. maximinoi* families from the best provenances averaged 20 m^3 of wood/ha/year, a 67% difference (Gapare, 2000). In South Africa, *P. tecunumanii* was recommended as an alternative exotic plantation species due to its high growth rate (Gapare, 2000) and good wood properties (Ximba and de Jager, 2000). It was also reported to outgrow *P. oocarpa* in Zimbabwe (Nyoka and Barnes, 1995) and indicated to have the potential to replace *P. patula* in Malawi as the most important industrial pine (Munthali and Stewart, 1998). It may be thought that the experimental design with linear plots may have influenced the observed yield in this study, making it larger than what would be expected from uniform plantations. The two *P.* patula trials disqualify this since one was made of linear and another square plots and their yield from both trials were comparable. The slightly higher growth rate (the difference in MAI was found to be 1 m^3/ha/year at 15 years) in the trial with square plots than in the one with linear plots may only be due to differences in site conditions, which more favourable on the former site than on the latter.

For *P. tecunumanii,* sources from Guatemala indicated superiority in volume production and therefore should be represented more in future afforestation programmes. The growth rate of *P. patula* in this study is poorer than that reported in South Africa except on some sites. The rate in South Africa is said to be 13.9-32 m^3/ha/year at nine and 12 years respectively (Poynton, 1979). The same author reports a MAI ranging from 17.3-33.2 m^3 for the species at 20 and 18 years respectively in Swaziland.

The existence of highly significant differences between seed sources indicates the potential for increased gains through selection and breeding. Improvements with *P. patula* is reported to have been successful in South Africa in both stem form and growth, with genetic gains in volume of 10-18% in seed orchard mixes and up to 40% for the best families (Stranger, 1998).

The promising sources for *P. patula* identified in this study include: Rancho Thacotha (8) (Mexico), DR de Wet FRS (27) (South Africa), DAN 5208 Zomba Plateau (3) (Malawi), Chimanimani (commercial lot) (13) (Zimbabwe), Stapleford (17) and Stapleford (commercial lot) (12) (Zimbabwe) and Kiamweri (21) (Kenya). The good growth of African sources may be exploited by introducing these together with the best of Mexican sources so as to increase the genetic base. Although there were no significant differences on site II for the species, the growth was good and all seed sources therefore can be recommended under the site conditions. Further studies may be established on site II using more sources including those from local as well as from other African countries (which were not tested in this trial) together with the Mexican sources.

The observed lack of correlation between one-year height and 16-year height, and the existence of strong correlation between four-year height and 16-year height growth on site I is similar to that observed in Kenya on *P. oocarpa.* Here, juvenile-mature correlation is reported to be unstable until at five years when provenance superiority emerges (Chagala and Gibson, 1984). As pointed out earlier, assuming positive relationship between genetic and phenotypic correlations, four-year height may be used as predictor of 16-year or older heights in this species. Again, this together with the observed inter-trait correlations may allow for early selection of superior seed lots. The significance of this early selection is that genetic gains can possibly be obtained at an earlier age, thus speeding up tree improvement programmes for the species. Although early selection may be a risk in tree breeding, it may probably contribute to the reduction of a breeding programme period for a particular tree species. A major reason for the apparent low returns on investments in tree growing originates from the long delay between the introduction of the technology in practice and the obtaining of the financial benefits at harvest (Sedjo, 1999).

P. caribaea and *P. kesiya* have proved to be poorly adapted to the local conditions. Only if resources were available would the species be retested since the poor site conditions as well as lack of thinning (*P. kesiya* was thinned only once) may have contributed to the failure to express their growth potential.

The observed very high growth rates and yields of some pines which even exceed that indicated by fast growing hardwood species (eucalypts) in this study was unexpected. Since the pine trials (except that of *P. kesiya*) were not thinned at all, while the eucalypt trials were thinned once (with a thinning intensity of 30%), one would expect even higher growth rates than those reported, if the trials had been thinned. Although *P. tecunumanii* is reported to show high growth rate and good wood properties (Ximba and de Jager, 2000), it would still be important to investigate if the wood properties of *P. maximinoi* and *P. tecunumanii* are not affected by their fast growth. The relationship between growth rate and wood properties such as wood density is very important. If one genetically selects for high growth rate, and if genetic correlation between density of wood and the growth rate was negative (wood density was observed to negatively correlate with growth phenotypically in *G. robusta* in this study at eight years), one would unintentionally select for low wood density as well.

Most of the conifers with dense wood, especially the hard pines, are reported to have little or no meaningful relationship between growth rate and specific gravity (Zobel and Jackson, 1995). Report on extensive references covering the interrelationships of growth rates and wood density for hard pines is given by Zobel and van Buijtenen (1989). Of the 59 studies, 35 showed no relationship between growth rate and specific gravity, nine exhibited small correlations, while 11 showed a significant reduction in specific gravity with faster growth rate, and only four showed a higher specific gravity for the fastest growing trees (Zobel and van Buijtenen, 1989).

The high rates of growth shown by some species in this study indicate a peculiar adaptation of these species to the tropical conditions. Very good tropical and sub tropical adaptation was reported for *E. urophylla* in some places. Spectacular growth rate (83 m^3/ha/year) was reported at Mangombe in Cameroon (Eldridge *et al.*, 1994). Of the locational variables, altitude may be playing a greater role to the observed adaptability than the latitude. This can be supported by observations reported for *Grevillea robusta* in Rwanda (Kalinganire, 1992) and that on *Pinus patula* in South Africa (Schutz, 1990). The authors observed significantly large influence of altitude and non significant one from latitude on species performance.

This study clearly indicates that there is a high potential for improved timber production in Rwanda through introductions of fast growing exotic species as demonstrated by *E. saligna, E. urophylla, P. maximinoi* and *P. tecunumanii.* Resources may therefore be focused on these species so as to exploit their high yield for improved timber production. The presence of genetic variation between seed sources in some species indicates the possibility for improvements and genetic gains through tree breeding activities. Strong age-age and trait-trait correlations observed in most of the tested species represents the possibility of predicting mature tree growth at a specified age as well as selection of superior seedlots using juvenile growth.

Apart from the understanding of superior seed sources for potential afforestation with exotic tree species, availability of improved seed or germplasm is a major constraint. A strategic tree improvement programme for Rwanda would therefore consider the production of appropriate seed for planting. In executing seed procurement for current plantation needs, collections from the best seed sources for potential afforestation species need to be made so as to obtain superior germplasm. Collection can be made from both external as well as local sources through mass selection. Commercial plantations and seed production areas can be established simultaneously so as to try to meet seed demand for future afforestation programmes. The stands for seed production can be selectively thinned to firstly eliminate poor individuals and secondly to provide more space to encourage bigger crowns for more seed production. In this respect, an initial species improvement programme such as that suggested for *G. robusta* in East Africa by Harwood and Owino (1992) can be adopted in Rwanda. In the programme, a stand is established for genetic improvement studies and converted into a seed production area through specific management practices (illustrated in Appendix 2).

Apart from being comparatively cheap due to the utilization of local labour, seed produced locally may be likely to develop trees that are better adapted to the local environment than the imported ones. It is estimated that 7.5 kg/ha can be produced by using a good selected stand of 150 trees/ha in *P. caribaea* in Venezuela (Segundo, 1981). Assuming a germination of 50%, the author further estimates the number of plantable seedlings/kg to be 125,000 (=9,375,000 seedlings/ha). In *G. robusta,*

healthy trees grown at a spacing of 5 m x 5 m or greater should produce at least 100g of seed/year on average (=40 kg of seed/ha), from eight to 10 years in an environment favourable for seed production, i.e. dry and warm climate, with 700-1000 mm mean annual precipitation and 20^0 C mean annual temperature (Harwood and Owino, 1992). CGF uses an average 30,500 plantable seedlings/kg for *G. robusta*. Using one year`s seed yield/ha at the above rate, 1,220,000 seedlings may be obtained.

Selective thinning would allow for the removal of inferior phenotypes leading to the managing of the remaining trees for seed production in genetic resource stands. A decision whether to include individuals from range wide collections in one trial or grouping them into provenance sub groupings will depend on the extent of variation in the species as well as the variation of conditions in the introduction sites and the corresponding quality to be bred for.

Seedling seed orchards can be established using genetically superior material. Progressive establishment of new orchards (Nikles and Spidy, 1973), at an interval of three-four years, provides the opportunity to improve genetic composition and provide replacement for earlier orchards in which the trees have become too tall and thus costly seed collection (Nikles, 1977). Clones can be selected from the species range, locally or from any other source where improved material exists. In this respect, Rwanda can make use of improved material for *Eucalyptus* and *Pinus* species from South Africa and Zimbabwe, together with collections from the species` natural range.

Under long-term tree improvement strategy, locally broad bases of superior or potentially superior populations need to be established. These are also established through selections from existing superior populations as well as from external sources such as natural populations, land races or from improved material where they exist. To further obtain gains, hybridisation can be made among related species. Individuals selected from locally adapted populations can be crossed with pollen from other local or external populations of superior sources identified through studies. Some *Eucalyptus* species are reported to have given significant good results in this regard.

E. tereticornis is said to hybridise with *E. alba, E. camaldulensis* and *E. grandis. P. patula* and some other pines (including *P. oocarpa* and *P. tecunumanii* among others) appear to be highly correlated to their crossability (as illustrated by close genetic distances between them), and *P. patula* can therefore be easily crossed with *P. oocarpa* and *P. tecunumanii* (Dvorak, 2000).

Although the findings obtained have achieved the objectives of the study, some gaps have been identified which require further research to complement to what have been achieved. The following recommendations can contribute to the better coverage of the gaps:

- Due to their highly promising results, *E. saligna, E. urophylla, P. maximinoi* and *P. tecunumanii* are recommended for plantation purposes. Some plantations of these species may be used as seed production stands in order to ensure the availability of seed for future plantation programmes.

- Since only age-age and trait-trait phenotypic correlations were studied, it would be useful to set trials so as to determine genetic correlations in order to obtain more reliable results. Studies on genotype x environment interaction may also contribute to the better understanding of the relationships.

- Wood properties of the pines observed to be fast growing in this study might be tested to assure that selection for fast growth will not affect specific gravity.

- In order to foster timber production in Rwanda, importation of germplasm from improved sources in other countries is recommended. Germplasm for some *Eucalyptus* and *Pinus* species from South Africa and Zimbabwe can be used. Development of successful hybrids may also be attempted through crossing of related species.

- For the purpose of increasing species diversity, introduction of other tropical exotic species such as *E. deglupta* and *P. oocarpa* may be attempted. Evaluation of important timber species locally planted but not already studied as regards to their performance may be done. Species like *E. grandis* and *E. camaldulensis* may be studied in this regard.

- Being one of the best upper storey, exotic agroforestry tree species, *G. robusta* needs to be retained and improved to develop strains that are adapted to various agro-ecological zones of the country.

- In depth studies of the relationship between seed sources and locational variables could be done so as to investigate the effect of altitude on the tropical adaptability of exotic species naturally growing in higher latitude areas.

- Sources of seed from high altitude zones in the range of *G. robusta* may be tested on high altitude sites in Rwanda so as to study the flowering and seeding capacity, which is currently a constraint.

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7. APPENDICES

Table 1: Correlation matrix for seed source mean growth in relation to locational variables of sites of origin.

Example: *Pinus kesiya* and *P. patula* I

Species	Trait	Pearson Correlation coefficients							
		Lat	Long	Alt (m)	*Adlat1	Adlat2	Adlat3	Adlat4	Adlat5
P. kesiya	DBH	-0.3105	-0.1123	0.0522	-0.2907	-0.3007	-0.3040	-0.3056	-0.3085
		(0.3826)	(0.4077)	(0.8860)	(0.4152)	(0.3985)	(0.3931)	(0.3905)	(0.3857)
P. kesiya	Height	-0.2463	-0.2951	-0.0686	-0.2422	-0.2445	-0.2452	-0.2455	-0.2460
		(0.4926)	(0.4077)	(0.8507)	(0.5002)	(0.4960)	(0.4947)	(0.4942)	(0.4933)
P. patula	DBH	0.1938	-0.2540	-0.0057	-0.1187	-0.0769	-0.0182	0.0451	0.1087
		(0.4130)	(0.2798)	(0.9803)	(0.6181)	(0.7472)	(0.9394)	(0.8501)	(0.6481)
P. patula	Height	-0.0085	-0.0701	-0.2552	0.0519	0.0573	0.0589	0.0542	0.0502
		(0.9717)	(0.7691)	(0.2642)	(0.8279)	(0.8105)	(0.8052)	(0.8204)	(0.8333)

Correlation coefficients are not significantly different (P>0.05). *Adlat=adjusted latitude. Figures in parentheses indicate probabilities.

Appendix 2: Nominal design and management details for *G. robusta* provenance/progeny trial to be converted to seedling seed orchard – after Harwood and Owino (1992.).

- Total of 150 families (130 Australian, 20 selected locally).
- Isolation distance of 1 km from other *G. robusta*.
- Two tree row plots, incomplete block design if resources of skilled labour permit, if not, a randomised complete block design to be used.

  -300 trees per replicate.

  -10 replications.
- Initial spacing 5m between rows, 1.8m within rows (1111 trees/ha).

-Bock size: 50 x 54 m^2 (10 rows, 30 trees/row).

-Block = 0.27ha.

-Total size of trial including perimeter guard row = 2.8 ha.

- Fertilizer as appropriate (micronutrient such as boron, may be required).

  Full weed control.

- First assessment of diameter, height and stem form at three years.

  -Selective thinning to 150 stem/rep. (=555 stems/ha) at three-four years. Only one individual of each family retained per replicate (mean height = 6m).

- Second assessment of diameter, height and stem form at five-six years.

  -Selective thinning to 50 stems/rep. (=185 stems/ha) at six years (mean height =10-12m).

- Flowering and seed production should start at age six-eight years in favourable environments.

- Thin to 100 stems/ha at age 12-15.

Appendix 3: Abbreviations

- ACIAR: Australian Centre for International Agricultural Research

- CAMCORE: Central American and Mexican Coniferous Resource Cooperation

- CE: Communauté Européenne

- CGF: Centrale des Graines Forestières
- CSIR: Council for Scientific and Industrial Research
- CSIRO: Commonwealth Scientific and Industrial Research Organization
- DANIDA: Danish International Development Agency
- FAO: United Nations Food and Agricultural Organization
- ICRAF: International Centre for Research in Agroforestry
- ISAR: Institut des Sciences Agronomiques du Rwanda
- IUFRO: International Union of Forestry Research Organizations
- MINAGRI: Ministère de l`Agriculture, de l`Elevage et des Forêts
- OECD: Organization for Economic Cooperation and Development
- PASAR: Projet d`Appui à la Sécurité Alimentaire au Rwanda
- SAFCOL: South African Forestry Company Limited